

A REVIEW OF SALINITY PROBLEMS OF ORGANISMS IN UNITED STATES COASTAL AREAS SUBJECT TO THE EFFECTS OF ENGINEERING WORKS¹

by

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ABSTRACT

The nongaseous substances that normally move in and out of cells are metabolites, water and salts. The common salts in water determine its salinity, and the definition of sea water salinity and its composition are discussed. The relationships of salinity to all phyla of animals living in the coastal waters are reviewed, with emphasis on the estuaries of the Gulf and Atlantic coasts of the United States, which are particularly influenced by coastal engineering works and changes of salinity caused thereby.

The fauna of estuaries is made up of a few brackish water species which complete their life cycles there, marine species which spend only a part of their life cycles there and which have definite low-salinity limits, a few anadromous species passing through, and a few fresh water species with high salinity limits. Organisms of marine origin are dominant. Floods and drought periods, resulting in severe osmotic changes, may kill organisms or result in drastic changes of the biota, which may take extended time to reestablish itself, if the conditions return to normal.

Many invertebrate animals have few mechanisms for controlling the movement of waters and salts across their external membranes and thus are osmotic conformers. Species that cannot withstand wide salinity change are said to be stenohaline, but many species can tolerate rather wide changes; they have broad tolerance at a cellular level. Osmoregulators exhibit considerable control of their internal salinity by excretory mechanisms and permeability control of the body surface to water and salts. In general, the worms and molluscs are more often osmoconformers than the crustaceans, the latter having greater control over their internal osmotic environment than other invertebrate groups. Effects upon different stages of life history are different, but in general the limiting effects of salinity and other environmental factors bear upon the reproductive stages of the young. The limits of salinities are nearly always on the lower side with regard to estuarine organisms. Aside from osmotic adjustments, animals react to salinity changes by closing their shells, closing their burrows, burying in the bottom where interstitial water has higher salinity, or motile forms simply move out. In spite of these adjustments, none may be successful during large floods.

The salinity relationships of all phyla are reviewed, even though some of them are unimportant parts of the marine populations. Dinoflagellate Protozoa which cause red tides

¹This paper is modified from a report that was prepared by the Gulf Coast Research Laboratory under Contract No. DACW39-72-C-0003 with the U. S. Army Engineer Waterways Experiment Station (WES) and Contract No. DACW73-70-C-0004 with the Department of the Army, Office of the Chief of Engineers (OCE) (Gunter, Ballard and Venkataramiah 1973). Preparation of that state-of-knowledge summary was initiated on the recommendation of the OCE Estuarine Ecological Consultants Board in an Interim Report entitled "Effects of Engineering Activities on Coastal Ecology" (Cronin, Gunter and Hopkins 1971). The report was published by the Waterways Experiment Station.

have precise salinity requirements and their outbreaks would be subject to control if reservoirs of fresh water were available. Sponges are generally high salinity organisms and not often damaged by low salinity. All the worms, including several phyla and the rather advanced Annelida, and the Mollusca are weakly motile at best and are thus subject to extermination by heavy floods in estuaries. However, most of these animals have short life cycles and their populations are quickly reestablished when the salinity regime returns to normal.

The dominant invertebrates in estuaries are crustaceans. The larger species are generally motile and not subject to catastrophic damage. Nevertheless, the lower limits of toleration of most species are quite limited and even a change of half part per thousand salinity will cause changes in the range in many species. If the salinity gradient falls, species drop out of the complex because their lower limits are reached, with the numbers of species becoming less in lower salinities.

There is an estuarine life history among the higher crustaceans such as shrimp and crabs which is also applicable to the fishes, and which is closely related to salinity. The adults spawn in high salinities of the open ocean and the young come back into the estuaries to raise. The young apparently prefer the lower salinities that the species will tolerate; and they move back out to sea as they grow, thus bringing about a correlation with rising salinity and increase in size, which may be quite precise as in the case of the commercial shrimp of the Gulf coast.

Although catastrophic changes in salinity are quite important to populations, the day-to-day generally normal salinity regimes also play a great part in determining the population picture of an estuary. Ninety-eight per cent of all the commercial fishery production in the Gulf of Mexico is from species connected with the estuary sometime in their life history.

The fishes of bays and sounds are made up of a relatively few species which spend their lives there, of semi-anadromous and anadromous fishes going from and coming to fresh water, of a few strays from fresh water, a few strays from the open ocean and a host of semi-cadromous species that undergo the marine-estuarine type of life history. Large specimens are found in higher salinity water for most species. Being strongly motile, few species are damaged by floods. The weakly motile amphioxus is the only chordate known to be destroyed in vast numbers by fresh water. The fishes are strong osmoregulators and in the changing salinity of the bays they regulate as fresh water fishes or marine fishes, depending upon whether or not the ambient salinity is higher or lower than that of the blood.

The salinity relations of salt water plants are less well known than those of the animals; however, a summary is given on what information we have concerning the flowering plants of the marshes and the totally submerged marine grasses along the Gulf coast.

Each separate bay, sound or estuary is an individual case with regard to salinity, but they can be appraised by biologists acquainted with the local fauna and flora so as to minimize and possibly even enhance their biotic potential in connection with salinity changes caused by engineering works.

GENERAL CONSIDERATIONS

The unitary or individualistic character of life has not been stated any clearer than it was by Claude Bernard when he said that organisms have enclosed themselves in a kind of hothouse, where the perpetual changes of external conditions cannot reach, and to this extent they are free and independent. He went on to say that all vital mechanisms have only one objective, that of preserving constant conditions of life in the internal environment. His succinct statement was, "Constancy of the internal medium is the condition of free life" (Bernard 1878).

The things which must be conserved for the maintenance of life are certain

physical and chemical limits and certain materials. Physical characteristics such as temperature and specific gravity are, of course, influenced and changed by the material exchange between the organism and the external environment, but we are concerned with the materials themselves which may be divided into water, electrolytes and non-electrolytes. Non-electrolytes, the metabolites, are used for the maintenance of structure or oxidized for the production of energy and their end products are cast out. A flux-equilibrium of these materials must be maintained. Here we are limited in attention to those materials, water and the electrolytes, which change within the organism when the external medium is changed in salinity. These changes involve the problems of osmotic regulations.

SALINITY

Salinity is the distinguishing characteristic of sea water, both physically and chemically. Pearse and Gunter (1957) have stated that "the most significant property of sea water in relation to the ecology and physiology of organisms depends on the fact that it is a complex solution of salts."

The salinity of the natural waters at the margins of the seas of this country and its cycles and natural fluctuations are changed or modified by large public works constructed there by the Corps of Engineers or by various agencies to which the Corps issues permits. The ecology of these areas is coming in for ever-closer scrutiny and it has become a matter of great importance to consider the salinity factor and its relation to marine organisms as influenced by large engineering works near the seas. The approach here is to review the biological information. The facts are sometimes technical but withal relatively simple.

The following account of the salinity of sea water is modified from Pearse and Gunter (1957) and other sources.

The oceans are primarily solutions of metallic salts, chiefly of sodium, magnesium, calcium, potassium and strontium. Organic materials are present in small amounts and atmospheric gases are held in the solution in varying amounts. Dissolved nitrate, phosphates and silicates are present in relatively minute and variable concentrations and are excluded from salinity determinations. The five chief metallic salts are in such constant proportions that a simple analysis of one component, the chloride, is theoretically sufficient in any ocean for determination of total salinity, specific gravity and proportions of the salts. Salinity has been officially defined by an International Commission as "the total amount of solid material in grams obtained in one kilogram of sea water, when all the carbonate has been converted to oxide, the bromine and iodine replaced by chlorine, and all the organic matter completely oxidized" (Sverdrup, Johnson and Fleming 1942). It is expressed in parts per thousand by the symbol ‰. Tables for determination of the chloride by titration and specific gravity by hydrometer have been prepared by Knudsen (1901) and they are standard tools of the oceanographer. Modern workers with more precise techniques are modifying the salinity tables, especially at the extremes of concentrations and dilutions, but generally this is only in the fourth decimal place of a part per thousand or less and is not of particular importance to this account.

Near the mouths of large rivers and their estuaries, where salinities are low, proportions of salts are slightly different from those of sea water. Some hard fresh waters are almost one part per thousand saline because of the carbonates and sulfates contained. On the other hand, the very low salt content of rivers along the State of Mississippi and Louisiana coasts cause coastal waters to have salinities lower than ordinary fresh water, but with salts still in the proportion of sea water (Price and Gunter 1964). Presumably, the Amazon River presents a similar case in its offshore waters.

The average salinity of ocean water is about 35 parts per thousand, but it is slightly different in the various oceans. The mid-Pacific surface salinity is 35.5 and the mid-Atlantic and the mid-Gulf is 37 and in the Red Sea it is about 40. Readings above 80 are quite common in the Sivash of Crimea and in the Laguna Madre of Texas and in the latter, during past years when there was less circulation than today, readings up to 112 were observed. In tropical shore ponds, which are only intermittently connected with the sea, readings equivalent to 155 parts per thousand have been observed; but certain salts settle out before these concentrations are attained and the saline proportions are not those of sea water. Higher than normal sea water salinities are not common in the world oceans or their margins, but they are found in certain restricted areas (Gunter 1967a).

Tables 1, 2 and 3 showing the salt content of sea water and some continental waters were taken from the various sources shown. Table 4 gives the major sea

Table 1.
Common Constituents of Sea Water and Typical Freshwaters, ‰

Ions	Normal Sea Water		Hard Fresh Water (3)	Soft Fresh Water (3)
	(1) (pH 8.17)	(2)		
Cl ⁻	19.630	18.9799	0.041	0.019
SO ₄ ²⁻	2.701	2.6486	0.025	0.007
Br ⁻	0.066	0.0646		
F ⁻	0.001	0.0013		
CO ₂	0.001			
H ₂ CO ₃				
HCO ₃ ⁻	0.116	0.1397		
CO ₃ ²⁻	0.012		0.119	0.012
H ₃ BO ₃	0.022	0.0260		
H ₂ BO ₃ ⁻	0.005			
Na ⁺	10.770	10.5561	0.021	0.016
Mg ⁺⁺	1.298	1.2720	0.014	0.00053
Ca ⁺⁺	0.408	0.4001	0.065	0.010
K ⁺	0.387	0.3800	0.016	...
Sr ⁺⁺	0.014	0.0133		
Salinity	35.161	34.3159	0.301	0.065

(1) From Rubey (1951); (2) From Sverdrup et al. (1942); (3) From Baldwin (1937).

Table 2.
Percentage of Dissolved Salts in Various Waters
After Rankama and Sahama (1950) and Clarke (1924)

Constituent	Sea Water	Lake and River Water (Average)	Jordan River Near Jericho	Dead Sea North End	Bear River Near Mouth	Great Salt Lake
CO ₃	0.41*	35.15	13.11	Trace	21.53	0.09
SO ₄	7.68	12.14	7.22	0.31	8.16	6.68
Cl	55.04	5.68	41.47	65.81	32.36	55.48
NO ₃	...	0.90	Trace
Ca	1.15	20.39	10.67	4.73	10.12	0.16
Mg	3.69	3.41	4.88	13.28	4.76	2.76
Na	30.62	5.79	18.11	11.65	20.54	33.17
K	1.10	2.12	1.14	1.85		1.66
Fe ₂ O ₃ , Al ₂ O ₃	...	2.75	1.45	...	2.53	...
SiO ₂	...	11.67	1.95	Trace
Sr, Br, H ₃ BO ₃	0.31
Br	2.37
	100	100	100	100	100	100
Salinity, ‰	35.0	.146	.770	192.15	.637	203.49

*As HCO₃—

Table 3.
Percentage of Dissolved Salts in Various Semi-enclosed and Inland Seas
Data from Clarke (1924); for the sea water, from Rankama and Sahama (1950)

Constituent	Sea Water	Baltic Sea	Eastern Mediterranean	Black Sea	Caspian Sea	Aral Sea
Cl	55.04	55.01	55.30	55.12	42.04	35.40
Br		0.13	0.16	0.18	0.05	0.03
SO ₄	7.68	8.00	7.72	7.47	23.99	30.98
CO ₃	0.41*	0.14	0.19	0.46	0.37	0.85
Na	30.62	30.47	30.51	30.46	24.70	22.62
K	1.10	0.96	1.12	1.16	0.54	0.54
Rb	...	0.04	0.02	0.02
Ca	1.15	1.67	1.19	1.41	2.29	4.02
Mg	3.69	3.53	3.81	3.74	5.97	5.50
Fe, SiO ₂ , PO ₄	...	0.05	...	0.03	...	0.04
Sr, Br, H ₃ BO ₃	0.31
	100	100	100	100	100	100
Salinity, ‰	35	7.21	38.36/41.15	18.2/22.2	12.94	10.84

*As HCO₃—

Table 4.

Major Seawater Constituents (Horne 1969)

Ions	Concentration, gm/kg of 35 ‰ seawater	Ions	Concentration, gm/kg of 35 ‰ seawater
Cl ⁻	19.353	K ⁺	0.387
Na ⁺	10.76	HCO ₃ ⁻	0.142
SO ₄ ²⁻	2.712	Br ⁻	0.067
Mg ²⁺	1.294	Sr ²⁺	0.008
Ca ²⁺	0.413		

Table 5.

Main Components of Sea Water in the Form of Salts (Per m³ of Sea Water
of 35 ‰ Salinity and 20°C) (Neumann and Pierson 1966)

NaCl	28.014 kg
MgCl ₂	3.812
MgSO ₄	1.752
CaSO ₄	1.283
K ₂ SO ₄	0.816
CaCO ₃	0.122
K Br	0.101
SrSO ₄	0.028
H ₂ BO ₃	0.028

water components according to Horne (1969). Sea water is highly ionized and therefore the characteristics of the individual salts are somewhat masked in the regular solution. However, if the water is all evaporated the remaining salts are those shown in Table 5 according to Neumann and Pierson (1966). These are very close to the figures given by Dittmar (1884) in his reports of chemical studies of the ocean as determined by the Challenger expedition.

The salt content of sea water modifies its physical properties, some of which are of considerable ecological significance. The temperature of maximum density of pure water is 4°C, while at 35.5 parts per thousand it is lowered to minus 3.8°C. The freezing temperature of water declines with increased salinity and at 35.5 parts per thousand this value is about minus 1.96°C, the initial freezing point at which a few ice crystals appear. Because of these facts earlier workers used the determination of freezing point lowering to measure the amounts of salts in the fluids of organisms. This method is still used where total osmotic pressure alone is to be determined.

WATER

Water is essential to all life because its physical and chemical attributes make it absolutely necessary to protoplasm and indeed it is incorporated in all living

substance. It is the chief road or avenue by which chemical and physical processes travel in living material. It serves as a solvent necessary for the chemical reactions involved in cellular metabolism and it acts as an ionizing agent. The properties of water are too extensive to be discussed here and understanding must of necessity be assumed, along with knowledge of osmosis.

Water must be present in the proper amount so that there is neither excessive swelling nor shrinking of the cell or other effects connected with its solvent function, specific heat properties, etc. Salts are also necessary to living cells and must be maintained in proper proportions for normal functioning of the cells. The relative amounts of salts and water determine the osmotic pressure of biological fluids and all living organisms face the problem of maintaining a proper water-salt balance.

Terrestrial animals must retain water; that is, they must have some mechanism for counteracting a tendency toward water loss through evaporation. All fresh water and salt water organisms have a problem, too, because even though immersed in water they are not usually in osmotic balance. Many marine and parasitic species are isosmotic with their media, but others face an osmotic problem due to differences in concentration of their body fluids and the surrounding medium. Fresh water animals must exclude water that tends to move into their bodies or remove it. They must also have some means of counteracting the loss of salts to the dilute medium. All animals that live in sea water of a salinity higher than their blood tend to lose water. In the relatively few animals that live in hypersaline waters, above sea water salinity, the tendency to lose water is greatest. Between these two extremes a variety of animals live in the waters of bays and sounds, where they are affected by salinity changes.

THE ESTUARINE ENVIRONMENT AND SALINITY

Salinity and its effects on living things are especially noticeable and important along the margins of the seas, where it sometimes varies greatly in both space and time. This area includes the coastal marshes, bays and estuaries, the importance of which has been much emphasized in recent years.

Estuaries form a large portion of the sea immediately adjacent to land. They are areas where sea water is measurably diluted with fresh water from land drainage. Salinity conditions are unstable because of variations in the relative amounts of fresh and salt water present, dependent on variable drainage and tidal effects. Salinity varies horizontally as the tide moves back and forth and as varying amounts of fresh water flow into the estuary. There is a general pattern of increasing salinity from the mainland shore seaward but the gradient is not always the same, not only because of the relative amounts of fresh and sea water present at any one time, but also because of the effects of winds and currents.

There are also vertical variations in salinity as the lighter fresher water generally overrides the denser salt water. In some estuaries there is distinct layering, but this type of gradient can also be affected by the mixing action of tides and currents and even by the shape of the basin. Estuaries, being relatively shallow and next to land,

are subject to atmospheric temperature changes which interact with salinity to influence distribution of animal life.

A large part of the coastline of the United States is bordered by estuaries and lagoons where fresh and salt water mix in varying proportions. Estuaries and lagoons are generally enclosed or semi-enclosed by peninsulas or barrier islands. Emery (1967) estimates that 80–90% of the Atlantic and the Gulf of Mexico coasts of the United States and 10–20% of the Pacific coast are bordered by lagoons and estuaries. They are generally called bays or sounds and sometimes "rivers" in North America and seldom estuaries. There is no sharp distinction between estuaries and lagoons but the latter is generally low in fresh-water influx and is considered to be more stable and saline and to support a more indigenous fauna (Caspers 1967). There is one hypersaline lagoon in south Texas and northern Mexico representing a relatively small area (see Gunter 1967a).

The fauna of an estuary is made up of three general categories of animals: (1) a relatively few typically brackish water species that can withstand wide changes in salinity and which complete their life cycles in the estuary, (2) many marine species that are able to live in unstable conditions but with low-salinity limits, including species that spend only a part of their life cycles in the estuary, (3) and a very few fresh water species but with high-salinity limits (Potts and Parry 1964a, Gunter 1967a). The senior author has emphasized in several publications that organisms of marine origin dominate the estuarine fauna even at very low salinities (see Gunter and Shell 1958).

Ordinary day-to-day variations in salinity do not normally disturb the composition of the fauna, since the characteristic animals of an estuary are adapted to such variations. Motile forms may move about somewhat and sessile species may withdraw temporarily into shells and tubes. Seasonal changes in salinity, interacting with temperature, however, can cause widespread and characteristic fluctuations of the fauna as certain species move in and out with advance and retreat of high-salinity waters caused by seasonal variations in rainfall. Gunter et al. (1964) pointed out, for example, that there is maximum invasion of the bays of the northern Gulf of Mexico by marine species in the dry fall season. Non-periodic and unpredictable severe conditions resulting in unusual osmotic conditions such as severe floods or prolonged drought can produce major catastrophes, killing off many species and causing others to move out of the estuary. In such cases it may take an extended period of time for the fauna to reestablish itself (Hoese 1960).

Degree of motility and method of osmoregulation can be important for survival in severe or sudden salinity changes. The influx of large amounts of fresh water on nonmotile or feebly motile species can be fatal. Large increases in salinity can also result in changes in the composition of the fauna. Estuarine motile animals can often withstand full sea water but preferentially choose lower salinities and so move at times of higher salinities.

Gunter (1961) has shown that on the northern Gulf of Mexico coast, the most important fishery region of North America, 98% of the fishery animals are connected at some stage of their life history with the estuaries. McHugh (1966) has shown that the American Atlantic fisheries are 63% estuarine dependent.

The famous New England and Canadian fisheries north of Cape Cod are based on the cod and its relatives from the offshore, high salinity banks. This fishery and that for the tuna are the only ones of consequence in North America which depend upon non-estuarine species. In northern Canada, the Pacific Northwest of the United States, western Canada and Alaska the fisheries are dominated by the trouts and salmons (Family Salmonidae) many if not most of which are anadromous or semi-anadromous and thus euryhaline. This same dominance of the salmonids formerly extended south to the Sacramento River and San Francisco Bay, but with the damming of the Columbia and the Sacramento tributaries the salmonids are fading in the southern part of their former realm.

It is clear from these remarks that the fisheries of North America are dominated by species with estuarine connections. This holds true for both sports and commercial fisheries, which overlap in species in many cases.

For a modern and recent summary account of the physical and chemical characteristics of estuaries the reader is referred to Abbott, Dawson and Oppenheimer (1971). Except for some questionable salinity limits given for the oyster, this is an excellent account.

Estuaries have been termed mixing bowls and even depositories for the materials that are brought down from the land. Even so, it should be held in mind that most of the material transported from land passes on through an estuary. For instance, the amount of sediment passing through an estuary during its lifetime may be over a hundred times the amount of sediment it would take to fill it completely (see Gunter, Mackin and Ingle 1964).

Pritchard (1951) has shown that salt water in bays in the northern hemisphere penetrates farther to the right, flowing in, due to rotation of the Earth. The cause is known as Coriolis force. This leads to a differential distribution of marine organisms on the opposite shores of the bays but the situation is not well documented as Emery and Stevenson (1957) have pointed out. Cowles (1930) recorded stomatopods farther in on the east side of Chesapeake Bay than on the western shore. Similarly Loesch (1965) found penaeid shrimp larvae differentially distributed in Mobile Bay. Sergerstråle (1957) has given similar information on the Baltic Sea.

A SUMMARY OF THE INFLUENCE OF SALINITY ON MARINE INVERTEBRATES

Many invertebrate animals have very little mechanism for controlling or counteracting osmotic movement of water, and the blood is nearly isosmotic with the surrounding water over the entire range tolerated. When such an animal is in a medium more dilute than its body fluids, water moves in through the body membranes and changes the concentration of body fluids until equilibration is reached. Conversely, when an animal is placed in a medium having a higher concentration than its body fluids, water will move out through the body membranes, thereby concentrating the body fluids, until an equilibrium is reached. Salts may also move in and out, but the end result is a change of the body fluids to a concentration approximately equal to that of the surrounding water. Such animals are termed

conformers or osmoconformers. Osmoregulation in such cases would seem to be largely a matter of tolerance at cellular levels.

Conformers vary greatly in their tolerance to dilution. If they have a very low tolerance they are, of necessity, confined to a very narrow salinity range. Such animals are said to be stenohaline. Most strictly marine animals are stenohaline. If conformers can withstand some dilution of their body fluids they can have a more extended range into regions of lower salinities. There are wide variations among species in the degree of dilution tolerated but there is always a limit, and the environmental range of such animals is limited by the degree of toleration. Animals with a wide salinity range are termed euryhaline. The mussel *Mytilus edulis* is an example of a euryhaline conformer. It occurs in salinities ranging from 30 ‰ to 10 ‰ and even down to 4 ‰ in some areas (Conklin and Krogh 1938, Segerstråle 1957). The American oyster, *Croostostrea virginica*, is an even better example. It will live for weeks at salinities just above fresh water (Gunter 1953) and lives indefinitely in full sea water (Gunter and Geyer 1955). According to Kelley and Burbank (1972) the estuarine isopod *Cyathura polita* is normally tolerant of salinities between 0.5 and 32 per mille.

Most estuarine organisms are of marine origin (Gunter 1956b, 1961a, Pearse and Gunter 1957) and almost all of them can live in full sea water, but the lower limits of salinity are limiting or lethal.

In addition to dilution of body fluids, change in body volume is a problem that must be faced by osmoconformers and is a factor involved in determining the salinity range tolerated. Animals vary in their permeability to salts and water. If they are permeable to both salts and water they may be able to withstand lower salinities than if they are permeable to water but fairly impermeable to salts. In the former case, although there may be an initial swelling on exposure to dilute media, equilibration will soon be reached as osmotic intake of water is accompanied by outward diffusion of salts. If salts do not move out fast enough and if there is no mechanism for excreting excess water, then the animal has no means of volume control and its salinity range is determined not only by its tolerance to internal dilution but also by the rate of salt loss. Two closely related species of polychaete worms illustrate the effect of differences in salt loss very well. When *Nereis diversicolor* is placed in 20% sea water it swells at first but begins to lose weight slowly until it regains nearly its original volume. On the other hand, *Perinereis cultrifera* becomes swollen and inert in 20% sea water and remains swollen. *N. diversicolor* regulates its volume by loss of salt from its body, but salt is not lost to any extent from *P. cultrifera* (Beadle 1931, Ellis 1937, Scheer 1948).

A number of animals are osmoconformers but almost none are ionic conformers. The concentrations of specific ions differ in the internal and external fluids even in those forms whose total blood osmoconcentration is equivalent to that of the external medium (see Table 6). The coelomic fluid of echinoderms closely approximates sea water in composition but it contains a slightly higher concentration of potassium. Various examples are cited by Pearse and Gunter (1957, p. 136). In some groups such as the cephalopods and decapod crustaceans ionic regulation extends to most ions in the blood (Robertson 1949, 1953, 1960, Nicol 1967). Ionic

Table 6.

Composition of the Body Fluids of Some Invertebrate Marine Animals.
Values Are Expressed as a Percentage of the Corresponding Values
in Sea Water or in the Body Fluid Dialyzed Against Sea Water

Taken from Shaw (1960) from Various Sources.

Animal	Freezing-point Depression	Na	K	Ca	Mg	Cl	SO ₄
Echinoderms							
<i>Echinus esculentus</i>	100	100	102	101	100	100	101
<i>Holothuria tubulosa</i>	100	101	103	102	104	100	100
Annelid							
<i>Arenicola marina</i>	100	100	103	100	100	98	92
Mollusks							
<i>Mytilus edulis</i>	100	100	135	100	100	101	98
<i>Eledone cirrosa</i>	100	97	152	107	103	102	77
Arthropods							
<i>Homarus vulgaris</i>	100	110	85	131	14	101	32
<i>Carcinus maenas</i>	98-103	110	118	108	34	104	61
<i>Pachygrapsus marmoratus</i>	91	94	95	92	24	87	46
<i>Palaemon serratus</i>	74	79	70	115	22	74	9

exchanges take place by active transport across permeable body surfaces by mechanisms not fully understood, and the excretory organs, when present, may also be involved.

Some invertebrate animals have the ability to maintain their blood at some concentration different from that of the environment. Such animals are termed osmoregulators. The most successful regulators among the invertebrates are the arthropods, especially the crustaceans, but some annelid worms and a few other forms can maintain hyperosmoticity in dilute media.

There is great variation among species in the degree of regulation exhibited. Some regulators live in a rather constant environment and so maintain a rather constant blood concentration either hyperosmotic to the medium, as for example the freshwater crayfish *Astacus*, or hyposmotic to the medium, as for example the brine shrimp *Artemia*.

Other species are subjected to fluctuating osmotic conditions and so must constantly face changing gradients between their internal fluids and the external medium. Apparently no animal is able to maintain an absolutely constant internal concentration under such conditions. All show some degree of variation in blood concentration with changes in salinity and so must exhibit some degree of tolerance. In fact, some regulators tolerate as great a change in internal concentration as do many conformers (Lockwood 1962). Even so, the internal change can be held within narrower limits than that of the external medium or, in other words, the environmental range of osmoregulators can be greater than their internal tolerance range.

Tolerance to dilution of the body fluids does not imply equal tolerance to intracellular dilution. The cells must be protected to some extent against fluctuations in blood concentration in both conformers and in regulators. The concept of intracellular regulation or regulation at the cell-blood boundary has become recognized. In this connection Fingerman and Fairbanks (1956) have shown that the very internal or central internal media of the oyster, around the heart, change salinities more slowly than the peripheral areas when the external medium changes.

Cellular isosmoticity appears to be accomplished by or at least accompanied by regulation of the intracellular concentration of organic substances, principally amino acids. It has been demonstrated that a direct relationship exists between concentration of free amino acids in the tissues, blood osmoconcentration, and salinity of the medium, but the exact mechanisms responsible for variations in amino acids have not yet been determined (Duchâteau and Florkin 1955, Potts 1958, Allen 1961, Lynch and Wood 1966, Lockwood 1967).

Most marine invertebrates are in osmotic equilibrium with their environment, although much recent work shows that most of them are not in ionic equilibrium (see Shaw 1960). In most animals, both water and salts penetrate the membranes and semipermeability is never approached closely. Possibly the most important finding of recent work is the fact that most materials are actively transported by some means or another against a concentration gradient in osmoregulation. This process was originally referred to as electroendosmose. As Shaw (1960) has pointed out, a steady state between an organism and its environment may be far from an equilibrium and thus energy must be supplied to maintain it. For this reason the osmoregulatory powers of most marine organisms break down quickly when they are deprived of oxygen, even though recent work (see Kinne 1971) has shown that thermodynamic work done in osmoregulation is a very small percentage of the metabolism.

Schlieper (1930) first showed that most marine invertebrates are isosmotic with sea water, but he and other workers have shown that this applies more to the worms and molluscs, and the crustaceans have better osmoregulatory powers and are not so prone to be so isosmotic.

Some invertebrates protect themselves from unfavorable changes in salinity by behavior resulting in minimum exposure to the medium. Oysters and barnacles may make themselves relatively impermeable by closing their shells. Worms may bury themselves in the mud or seek crevices near the bottom where salinities are higher than in the overriding fresh water. Certain tube worms have been observed to cease irrigation movements and thus reduce to a minimum the mixing of water of the immediate environment with fresher water (Mangum 1964). Some hydrozoan coelenterates show structural changes that reduce the surface area exposed to the medium (Kinne 1964). Motile invertebrates may actively move to more favorable environments and some bury in the mud, but many are too small to escape sudden changes. Others may retreat to the bottom of deep burrows. Occasionally heavy freshets or floods will kill bottom burrowing organisms and large mortalities will take place (see Dawson 1965).

A consideration of salinity effects must be concerned with life cycles since

the requirements at different life stages may differ. Embryos and larvae may be more sensitive to unusual stresses than adults are (see Robertson 1957) and it is a general law (Shelford 1915) that the effects of environmental limits or extremes act on particular phases of life histories, often the reproductive stages or young. The early larvae of some estuarine species will not develop normally in low salinities and so the adults must migrate to high salinities to spawn (Sandoz and Rogers 1944, Costlow and Bookhout 1959). Adult white shrimp live in high salinities, but the young, postlarval shrimp apparently must reach low-salinity estuarine waters or most of them die (Viosca 1920, Weymouth et al., 1933).

Although various factors such as temperature, age, sex, and stage of molt may influence osmotic response (Baumburger and Olmsted 1928, Kinne 1963, Robertson 1960, Ballard and Abbott 1969), salinity, or concentration of the environment, is the basic factor determining blood salt concentration. Since invertebrates inhabit widely varying salinities, they have a variety of mechanisms for handling osmotic problems. Perhaps no environment is so demanding as the estuarine environment where there are seasonal and even daily fluctuations in salinity due to such factors as river discharge and tides, as well as seasonal and short-term changes in temperature which affect osmotic response. Animals living in such an environment must adjust to fluctuating osmotic conditions either by efficient osmoregulation or, perhaps, by a combination in which, although there is change in blood concentration with change in salinity, the internal variation is less than that of the external environment.

Life in an estuary appears to be rigorous, but the very variability is a constant feature, and estuarine species must be labile and euryhaline. Nonetheless, salinity can be a limiting factor, particularly on the lower side, and does affect the distribution of species (Gunter 1961a, Pearse and Gunter 1957, Potts and Parry 1964b and many previous papers). The upper salinity distribution limit may be ecological and behavioral rather than physiological. A number of brackish water species such as the polychaete worm, *Nereis diversicolor*, the shrimp, *Palaeomonetes varians*, and the oyster, *Crassostrea virginica*, can survive well in full sea water but they do not usually occur in the sea.

The lower salinity limit, on the other hand, is largely physiological. As the water in estuaries becomes more dilute, the number of species declines in the order of their decreasing ability to tolerate or regulate (Gunter 1961a, Prosser and Brown 1961). Enemy species and diseases similarly decline with lowering salinity, which is probably one reason the estuaries are primarily nursery grounds for so many important species. Similarly the increase of enemies and diseases with increasing salinity is one reason many organisms are not commonly found in high salinities which they can tolerate physiologically.

The present summary of the influence of salinity changes on invertebrates could be divided as follows: (1) the worms and lower organisms (2) the molluscs (3) the crustaceans (4) lophophorates and (5) deuterostomes, but the phyletic array is followed. Osmoregulating species have received the most attention, but studies have been made of degree of tolerance, ionic regulation, and cellular regulation in conformers as well. Since most strictly marine (offshore) species are isosmotic in a relatively constant environment, and since the present analysis is related to engineering changes in coastal areas, emphasis is placed on effects of varying salinity on

estuarine and coastal invertebrates which could be affected by such works. However, some general remarks will be made concerning the physiology of marine and freshwater species.

INFLUENCE OF SALINITY ON SPECIFIC INVERTEBRATE AND VERTEBRATE GROUPS

The Invertebrata include all animals without a notochord or backbone and are larger in numbers, species and biomass than the chordate animals which all people, including zoologists, are inclined to overrate in the Animal Kingdom.

These organisms are generally small and many of them are parasites or commensals of other animals. They are also extremely diverse and their natural history and physiology are not as well known as that of vertebrates in general. In this article we shall take up the larger groups of invertebrates roughly in a hierarchy proceeding from the simple to the complex as recognized by zoologists. Parasites are not considered here because the effect of salinity on the host species is always paramount.

A. PROTOZOA. These organisms may be defined as one-celled individuals which cannot manufacture their own food and must take it from the outside. Many species are parasitic and virtually nonmotile at most stages of their life history.

In spite of the purely animal character of a number of protozoans, some of them, especially the Flagellata, are so closely related to single-celled, purely plant-like organisms in their nutrition that separation of groups by clear-cut definitions are quite difficult. This presents no real problem, however, and is merely an indication of the close kinship of lower organisms.

The purely animal flagellates are sometimes of interest because of their ability to produce light, such as *Noctiluca*, when they bloom or swarm in large quantities, but they are not abundant in estuarine habitats and are osmotic conformers in high-salinity waters (see C. C. Davis 1953 and papers cited). There are certain shelled or naked amoebae living in low-salinity waters which are very much like freshwater forms except that they may lack a contractile vacuole. These organisms are crawlers and creepers and they are not numerous, at least in swarm numbers, and they are difficult to demonstrate.

Various members of the Ciliate, *Folliculina* and relatives, build little clear houses of chitinous material and attach themselves to hard substrata such as oyster shells, bryozoans, or hydroids and may be numerous seasonally in low-salinity estuarine areas (see Andrews 1915). They are known as bottle animalcules. Some ciliates devour larvae of valuable mollusks (Loosanoff 1959) and their ecological importance may be underestimated.

The radiolarian ooze of the deep sea and the foraminiferal ooze of the shallow sea and the chalk beds have been of considerable interest not only to the modern oceanographer but to the geologists who want to relate various geological strata to one another. But again we receive the impression that these organisms are abundant only in high-salinity waters and in fact there are few papers on living

Foraminifera in the bays. Those of the Gulf coast are listed by Waldron (1963). His work concerned Timbalier Bay in Louisiana and he concluded that upper bay (low-salinity waters) included mostly arenaceous species, while lower bay species included chiefly calcareous or marine species. Ayala-Castañares and Segura (1968) recorded the Foraminifera from the Laguna Madre of Tamaulipas, a dying lagoon only containing water following hurricane breaches of the barrier island, which rapidly becomes hypersaline or dies completely.

The Radiolaria are uncommon in estuarine waters and the Foraminifera are not abundant. Nevertheless, we must say that we do not know what part the Protozoa play in the living energy systems of bays and estuarine areas, but it may be assumed that large floods of fresh water will kill them out in untold millions. However, the rapidity of the life cycle is such that they probably replenish barren areas with great rapidity when salinities return to normal. Waldron (1963) said there were three or four population peaks per species in Timbalier Bay in ten months.

Some things are known about the osmotic relationship of the Protozoa. In general, their osmotic problems are the same as those of larger organisms, as it makes little difference if a living membrane is composed of one or many cells. Most protozoans maintain an internal concentration slightly hyperosmotic to the medium in brackish water. Some show an initial swelling when placed at lower salinities but will generally return to normal after a period of time. Papers cited by Davis (1953) give the salinity of the cell sap.

In freshwater Protozoa the contractile vacuole is considered to be an organelle of excretion of the waste products of metabolism, as well as a way of getting rid of excess water taken in by osmosis or in feeding. The latter idea is supported by the fact that certain marine amoebae have vacuoles only during times of active feeding (Nicol 1967). Rudzinska and Chambers (1951) found that the vacuolar output of a freshwater suctorian increased six times during feeding. Frequency of contraction is always greater in freshwater forms but may increase in marine forms placed in fresher water (Kalmus 1929). Many marine forms have no contractile vacuoles under normal conditions, but others do.

According to Shaw (1960) the cell sap of the freshwater Protozoa is much lower in salt content than that of some of the fishes or Crustacea. He shows in a table, p. 478, that some crustacean liquids may be 35 times as salty as the cell sap of *Spirostomum*, a ciliate. There are some indications that the cell membranes of the Protozoa are much more permeable to water than to salts. This fact, the low cell sap salinity, and the contractile vacuoles set the Protozoa off osmotically from all but some of the lowest Invertebrata.

Kinne (1971) has pointed out that resting stages, spores, and cysts of protozoans, hydrozoans and sponges have higher salinity tolerances than active stages and this is of great importance in enabling populations to survive periods of stress.

Kinne (1971, p. 832) cites papers showing that certain young stages of Protozoa and other invertebrates may tolerate abrupt salinity changes more easily than adults. But this work needs further investigation and is possibly connected somehow with the fact that adults are often in higher salinities than juveniles and young.

Very little is known of ionic regulations in the Protozoa, although they must have high capabilities in this regard to maintain cell sap at such different salinities from the blood of other invertebrates in the same water (Shaw 1960).

Some euryhaline Protozoa are good volume regulators at wide ranges of salinity, and although the contractile vacuole rate increases or decreases clearly with salinity changes (see Kanoshiro et al. 1969) some good volume regulators have no vacuoles. Krogh (1939) demonstrated quite a number of protozoan osmoconformers.

Harder (1968) has shown that certain Protozoa, *Noctiluca*, *Gymnodinium* and *Tinntinnopsis*, accumulate at discontinuity layers of sea water, which means that they can avoid certain densities to some extent.

The naked dinoflagellates which cause the so-called Red Tide are purely phytoplankton, called by the botanists Dinophyceae. Nevertheless, they are more often treated by zoologists, probably because these plankton blooms are lethal to many organisms. Small blooms in fresh water and on north temperate coasts have been known for a long time. These are mostly localized in bays and along our own northwest Pacific coast are generally caused by *Gonyaulax* (see Martin and Nelson 1929 and papers cited).

Gessner (1959) found that in Baltic and North Sea waters dinoflagellate species were about twice as common in salinities above 30 ‰ as at 0.25 to 6.0 ‰.

Some flagellates seem to have very wide ranges of salinity optima. Goyacheva (1969) said that the optimal salinity range was 20 to 40 ppt. for *Bodo marina*, and Hand, Collard and Davenport (1965) stated that *Gonyaulax* swam at high speed from 20 to 36 ppt. salinity, while *Gyrodinium* swam at above 225 microns per second from 8 to 41 ppt. The first species is littoral and *Gyrodinium* is lagoonal or estuarine in distribution. Certain flagellate species have been recommended for mass culture because of their tolerance in wide environmental conditions, including salinity (see Spektorova 1970).

The vast fish kills of the lower two-thirds of west Florida and occasionally a similar region of south Texas and northwest Mexico are caused by *Gymnodinium breve* Davis (Davis 1948) as was first shown by Gunter, Williams, Davis and Smith (1948). Much work has been done on this organism and it was reviewed by Rounsefell and Nelson (1966).

The above-cited papers summarize information on the Red Tide. It follows heavy drainage from land, which probably brings in some component as yet unknown, and a long spell of warm weather where the water temperatures approach 30°C, and a period of calm weather. The organisms may attain densities of 60,000,000 to the liter—enough to change the physical properties of the water and everything dies, including *G. breve*, either from lack of oxygen or auto intoxication. It is one of the major catastrophic mortalities of the sea, rivaling the Peruvian die-off, El Nino, which may well involve a Red Tide organism as the senior author has suggested before.

The salinities found at times of Florida blooms are between 31–35 ‰. At times following heavy rains a wide belt of such salinity may extend all along the

Florida coast. This may lead to extensive spread of the Red Tide. Small patches first begin in the lower bays and possibly they could be destroyed there by releases of fresh water in storage basins above. At present the Lake Okeechobee outlet through the Caloosahatchee River is the only one appropriate to the situation in west Florida and there is none in south Texas or Mexico.

The Florida Red Tide can be killed by low concentrations of copper sulphate, but so is everything else and the only feasible control method remaining is fresh water, if the water supply can be obtained.

B. PORIFERA or PARAZOA. This phylum of animals, the sponges, is one that most people have heard of and two verbs in English have been derived from it. It is generally considered to be the lowest group of the multicellular organisms and has no nervous, muscular or vascular systems, although there are single cells which carry on some muscle and nerve functions. Chiefly because the embryonic development of the germ layers does not correspond to that of the other multicellular organisms, the Metazoa, these animals are considered to be a branch aside from all others and are called Parazoa. Their flagella cells have collars around them and show a great similarity to the choanoflagellate Protozoa. There is nothing else in the Animal Kingdom like their internal interlacing skeleton of calcite or silicate spicules and sometimes horny fibers, from which comes the commercial sponge. Their organization is also quite different from the other invertebrates. There are various layers of tissues and essentially a sponge is a body of cells which draws water in through numerous pores by the action of flagellate cells, and casts the water into a central chamber and out through a single opening, the osculum.

There are about 3,000 species of sponges, with a few hundred in the fresh waters of the world and the remainder in the ocean from the surface to great depths.

Insofar as sponges have no vascular system or body cavities holding their own liquids and live with sea water both inside and out, osmotic studies can be only of a cellular nature, and apparently these are uncommon. Thus known salinity relationships derive almost solely from field observations, and few observers have taken salinities along with collections of sponges. Here we have gathered the few data from a wide literature.

Sponges are found chiefly in high salinity and clear waters; thus they are uncommon in estuarine waters, except for the boring sponge, *Cliona*, which is common on oyster beds and calcareous rocks which they perforate in moderate to high salinity waters. A few other genera of encrusting sponges, such as *Microciona* and *Haliclona* are found in the bays where there is a hard substratum and fairly high salinities.

The shallow offshore waters of the west Florida Peninsula to 350 feet in depth, southward through the Keys, during the first half of this century was one of the more prolific commercial sponge producing areas on Earth. These waters are clear, possibly because there is small land drainage, combined with the effect of high calcium content of this drainage. The industry was centered at Tarpon Springs and was devastated by a sponge disease in 1938-39 and the Red Tide in 1946-47. It has never recovered, due in part to the competition from synthetic sponges.

Nevertheless, large amounts of sponges still inhabit the clear warm waters of the west coast of Florida. In contrast, no sponges were reported by Gunter and Hall (1965) in the Caloosahatchee Estuary where the salinity ranges from 0.13 to 32.2 ppt. On the other hand, the offshore areas of Pine Island Sound and San Carlos Bay outside the Caloosahatchee, where the salinities were always around 30 ppt and above, sponges of several species formed the greater bulk of trawl catches, and this area was described as a "sponge reef."

Dawson and Smith (1953) reported commercial Florida sponges at salinities ranging from 28.5 to 36.6 ppt and averaging 34.6 at 35 stations. Storr (1964) stated that when the salinity dropped to 26.0 ppt following storms and heavy rains it was lethal to the Florida commercial sponges.

Sponges are relatively uncommon on the northern Gulf coast, probably due to the high turbidity of these waters as well as low salinities. *Haliclona* has been reported by Hopkins (1956) at 20.0 ppt in Texas and Louisiana. The most common habitat for these sponges seems to be the jetties of the passes, but *Microciona* has been reported on oysters in Aransas Bay, Texas, at salinities as low as 19.0 by Gunter (1955). The boring sponge *Cliona* sometimes damages living oysters and it is killed out by floods and freshets (see Gunter 1953). Salinity records are scarce for this species, but Hopkins (1956) says absence of *C. celata* on Louisiana oyster shells indicates salinities below 10.0 one-fourth of the time, while the absence of *C. trutta* indicates salinities below 10.0 half the time. Mrs. Harriet Perry has several collections of *Craniella* sp. from Dog Keys Pass, Mississippi, at salinities of 25.0 to 32.0 ppt.

Hopkins (1962) refined the salinity observations on four species of *Cliona* in Virginia and found that in waters ranging from 3 to 36 ppt the mean at the sample areas was 22.1 but the mean of salinities where species were caught were: *celata* 26.7, *vastifera* 22.8, *lobata* 19.1 and *trutta* 18.9.

Sponges feed upon minute organisms, bacteria or flagellates, or possibly dead organic materials, and they have some effect upon the environment in that way. They also shelter large numbers of crustaceans, worms and other organisms that live in cavities of the sponge. Otherwise they are not of great importance. Marine sponges are generally high salinity organisms and are easily killed out by freshets, but in general, they are not harmed often because they live mostly outside and beyond the lower bays or the low salinity effects. Nevertheless, heavy rainfall sometimes affects sponges in the ocean, if they are close to shore (Storr 1964).

C. MESOZOA. This peculiar group of organisms may be as aberrant and different from all other animals as the sponges are. They consist of a definite number of cells with no germ layers and no organ systems. They have the appearance of degenerate, ciliated flatworms and have a solid blastula; this and some life history features have led some workers to believe that they are degenerate trematodes, while others look upon them as inherently primitive. One group, the *Dicyymia*, live only in kidney tubes of octopuses and the other, the *Orthonecta*, are parasitic in the tissues and spaces of other marine invertebrates. As parasites or commensals their relations to salinity follow that of their hosts.

D. COELENTERATA or CNIDARIA. There are two phyla of diploblastic or two-layered animals, the coelenterates and ctenophores, commonly called jellyfish.

The Coelenterata all have stinging cells and live from fresh water to the deep seas. Their symmetry is generally radial. A number of species are simple hydroids, like *Hydra*, and some are fairly complicated medusae, with a nerve ring around the bell and with statocysts. There is also alternation of generations between hydroid and medusoid generations in many species. This group also includes the sea anemones, the soft corals (sea pens, sea fans and the like) and the hard corals or coral reefs. There are no blood or tissue spaces and all osmoregulation is cellular.

HYDROZOA AND SCYPHOZOA

Macallum (1903) reduced the large medusae, *Aurelia* and *Cyanea*, to a liquid and found a much higher potassium and much lower sulphate content than in the surrounding sea water. Robertson (1949) found low sulphate in the mesoglea of *Aurelia*, the jellylike substance between the cell layers of the jellyfish, but no higher potassium. Béthe (1908) showed that when the Mediterranean medusae, *Rhizostoma* and *Carmarina*, were subjected to 80% sea water for 48 hours there was no slowing of movements but in 75% sea water slowing took place in 30 minutes, and stopped entirely in one hour in 50% sea water.

Webb, Schimpe and Olmon (1972) found higher concentrations of free amino acids in the tissues of three common scyphozoans of Virginia waters at higher salinities.

The abundant scyphozoan jellyfishes of the bays of the South Atlantic and the Gulf coasts are *Aurelia aurita*, *Stomolophus meleagris* and *Chrysaora quinquecirrha*. The last species stings rather virulently and is considered to be quite a pest in Chesapeake Bay. In Texas waters along the Gulf shore *Pelagia noctiluca* is abundant in dry years (Sanders and Sanders 1963), and the dangerous cubomedusan, *Chiropsalmus quadrumanus*, become abundant in the bays (Guest 1959). Most of the time *Chrysaora* is most abundant in bay waters although *Aurelia* is the dominant medusa in some years (Gunter 1955). This species has been observed in Texas waters at 16.0 ppt saline (Gunter 1950) which is lower than recorded elsewhere, see Table 7. Franks et al. (1972) noted this discrepancy and reported *Aurelia* as taken only in Mississippi waters at high salinities.

The generally smaller hydrozoan medusa *Liriope tetraphylla* and *Bougainvillea* spp. are also abundant in Mississippi waters.

The siphonophore *Physalia physalis* is abundant in the open ocean, especially in the western Gulf and is quite evidently a high salinity organism.

Table 7 gives salinity ranges of common jellyfish taken at the Gulf Coast Research Laboratory during 1968-71 inclusive. This table and the information was furnished by Mr. David Burke.

In Mississippi Sound the greatest incidence of hydromedusae occurs at salinities of 25.1-30.0 ‰ as demonstrated in Table 7. There is a gradual

Table 7.

Some Salinity Ranges and Averages of Jellyfish on the Mississippi Coast from 1968 to 1971.

	Salinity Range ‰	Salinity Average ‰	Number of Specimens
Scyphozoa			
<i>Aurelia aurita</i>	29.2-31.0	29.3	343
<i>Cyanea capillata</i>	23.2-29.6	26.4	50
<i>Stomolophus meleagris</i>	19.4-25.7	24.8	285
<i>Pelagia noctiluca</i>	32.0-33.9	25.9	134
<i>Chrysaora quinquecirrha</i>	10.6-31.3	27.0	2,306
<i>Chiropsalmus quadrumanus</i>	18.2-34.0	27.0	329
<i>Hydrozoan medusae</i>
<i>Liriope tetraphylla</i>	27.5-32.5	28.4	46,971
<i>Persa incolorata</i>	25.0-35.0
<i>Nemopsis bachei</i>	7.5-32.5	16.4	1,003
<i>Bougainvillea</i> sp.	10.0-25.0	26.2	6,364
<i>Euphyllora gracilis</i>	17.0-35.5
Siphonophora			
<i>Physalia physalis</i>	28.2-37.6

decline with decreasing salinities, and a marked decline with increasing salinities. Under true marine conditions hydromedusae are apparently displaced ecologically by siphonophores, no species of which occur below 25 ‰ in Mississippi Sound.

Among the entire array of hydromedusae present in Mississippi Sound (54 species), only one species, *Liriope tetraphylla*, is apparently rigidly stenohaline, and is to be found between the limits of 27.5 and 32.5 ‰. A distribution more typical of hydromedusae is demonstrated by *Nemopsis bachei*, which occurs throughout a salinity range of 7.5-32.5 ‰.

Most Scyphozoa in Mississippi Sound are high salinity organisms. Exceptions to the above trend are exemplified by *Chrysaora quinquecirrha* which occurred throughout a range of 10.6 to 31.3 ‰, and *Chiropsalmus* which occurred throughout a range of 18.2-34.0 ‰. One specimen of the coronates, *Nausithoe punctata*, was collected at a salinity of 35.3 ‰.

The importance of the jellyfish to the living community is as predators. They live on the microplankton and animals ranging up to the size of small fishes. *Stomolophus* has no mouth and only hundreds of minute openings. On the other hand, the Portuguese man-of-war can capture fishes several inches long. Fraser (1969) made brief reference to reports on food studies of medusa, most of which are European, and presented results of his laboratory studies. He noted that larval fish are important food sources and presented evidence that medusae may consume from 50 to 15,000 larval fish during a lifetime, which he took to be about six weeks

in Newfoundland waters; the number consumed varied with species and size of the jellyfish.

There is no doubt that medusans of inshore waters consume vast numbers of small invertebrates and larvae and larval fishes, especially at times of their peak abundance, when some of the hydrozoan medusae, such as *Nemopsis bachei*, can be collected in Mississippi Sound by the jarfull by dipping overboard. Phillips, Burke and Keener (1969) have presented observations on the trophic importance of jellyfishes in Mississippi Sound, which are generally applicable to much of the east coast of the United States.

ANTHOZOA

The chief studies of the anemones of the south Atlantic and Gulf coasts, (Field 1949) and Carlgren and Hedgpeth (1952), make no mention of salinity distributions of those organisms but it is obvious that they are found near or in the passes to the ocean or the outside beaches. Christmas and Langley (1973) noted thirty-one *Calliactis polypus*, a species associated with hermit crabs, at salinities of approximately 22.5 to 33.5 ppt in Mississippi waters.

Dregol'Skaya (1961) determined how long cells of *Actinia equin* were maintained at temperatures of 38–42°C and different salinities. Anemones from the Black Sea (17.5 ‰) were acclimated to 35 ‰. This led to a 70% increase in heat resistance at all temperatures. This was higher than *Actinia* from the Barents Sea where the salinity is 35 ppt. Thus the difference in heat resistance of the two populations is not caused by salinity of the anemone's habitat.

Shoup (1932) found that *Metridium marginatum* in sea water at 30 ppt consumed less oxygen when the water was changed to 10, 15, 45 and 60 ppt sea water of M/2 or M/4 NaCl, KCl or CaCl₂. The greatest decreases were at 60 ppt. At 10 ppt the tentacles contracted about a third. Contraction also occurred in hypertonic sea water. At 60 ppt tentacles were completely withdrawn, mucous was secreted and the nematocysts were discharged. The anemones returned to normal after four hours in normal sea water.

The soft coral, *Leptogorgia setacea* and *Renilla mulleri*, are found in the shallow Gulf, sometimes in large quantities. The latter is more offshore, but *L. setacea* often washes up in windrows on Texas beaches. Gunter (1950) reported salinities ranging from 26.7 to 36.7 for *Renilla* in Texas. Less common species there are *L. hebes* and *Eugorgia virgulata*. In Mississippi waters Christmas and Langley (1973) reported taking 472 *Renilla* at salinities from about 19.0 to 35.5 ppt within the bay waters. In the open Gulf of Mississippi Franks et al. (1972) reported 16,808 specimens taken at a salinity range of 24.9–37.8. Bayer (1954) says a few species of the Alcyonaria can live where salinities are occasionally reduced but "are never found where appreciable dilution regularly occurs," p. 281.

Two hard corals, *Astrangia astreiformes* and *Oculina* sp., are sometimes found in the lower bays and shallow offshore waters in very small patches. Christmas and Langley (1973) have reported *Astrangia* in Mississippi Sound at a salinity of 24.4 ppt.

Coral reefs are not present on the northern Gulf coast and the closest one is Blanquilla Reef near Tampico (Moore 1958). Vaughan (1915) showed that Florida reef corals lived well in 80% sea water but died at 50% within 24 hours. These animals live in full sea water and it is generally assumed that they are never damaged by freshets or rain.

It is obvious from the above remarks that changes in salinities in coastal waters will have greatest influence on the coelenterate fauna through effects on the Hydrozoa and Scyphozoa, which are important as predators and sometimes annoyances to swimmers. The anemones, and especially the soft and hard corals, are rather poorly represented in estuarine or inshore waters and so are not generally exposed to salinity changes.

E. CTENOPHORA. These animals are all marine and they are biradially symmetrical. They come under the common name jellyfish, but are quite different from the Coelenterata in several ways. They do not have stinging cells but instead they have adhesive cells called colloblasts or "lasso" cells. There is some evidence that *Beroe ovata* does produce a toxin at the colloblasts. They swim by cilia in eight meridional bands. In spite of the fact that they seem to be among the most fragile organisms in the world, tearing under their own weight when removed from the water and being almost impossible to preserve, they are nevertheless very important predators upon small fishes and invertebrates and some workers have stated that the abundance of invertebrate plankton, including oyster larvae in the bays, is low when large numbers of ctenophores are present (Nelson 1925, Phillips et al. 1969). This predatory relationship to the plankton is the chief importance of these organisms to other animals in the coastal areas. Gudger (1943) has summarized some of the older literature on the fish-eating habits of ctenophores.

Ctenophores are also of considerable interest zoologically because certain genera are much like the flatworms in general appearance and anatomy, thus constituting something of a connecting link between the two phyla. One of these *Coeloplana* has lost all cilia and crawls on the substrate. It has been recorded in south Florida (Smith 1945).

There are no body spaces or lacunae in the Ctenophora and there is little literature on their adjustment to salinity changes. Lazareva (1961) found that changes between 10–20 ‰ salinity did not affect oxygen consumption of *Pleurobrachia pileus*, but variations outside this range lowered O₂ consumption. Wells, Ledingham and Gregory (1940) showed that cilia of the same animals were inhibited, followed by accommodation, after sudden changes of salinity either up or down.

The two species, *Mnemiopsis mccradyi* and *Beroe ovata*, are found from New England to the southern limits of the country and beyond, and practically always in the bays and sounds. They are both plankton consumers and the first is a prey of the latter. Sometimes they are so numerous in the bays that trawl catches are largely masses of ctenophore jelly in which individuals cannot be distinguished and other animals are difficult to pick out. Gunter (1950) reported these two ctenophores as being most abundant in Texas waters from October to December at salinities of

11.5 to 13.7 per mille. Whitten, Rosene and Hedgpeth (1950) noted large numbers of *Mnemiopsis* washed in among jetty rocks along ship channels. Christmas and Langley (1973) reported *Mnemiopsis* sometimes so abundant in Mississippi Sound that they made trawls and seines inoperable. Perry and Christmas (1973) noted ctenophore swarms from April through November in the Sound and they stated that by far the largest component of plankton volume was ctenophores. They found the greatest numbers between 5 and 20 parts per thousand saline, with no swarms at higher or lower salinities. The minimum salinity at which the species were taken was 5.6 ppt and the maximum was 33.3. The average salinity was 16.8.

Very small tentaculate ctenophores, sometimes called cydippid larvae, have been taken even in tributaries of Mississippi Sound, and so it seems that the whole development may be completed in estuarine waters (David Burke, personal communication). This is contrary to previous ideas that early development and breeding in the Ctenophora is always in the oceanic environment.

F. PLATYHELMINTHES. This phylum consists of the free-living turbellarians, and two parasitic groups, the trematodes and cestodes. It is the lowest phylum with a definitive mesoderm, although claims have been made for the ctenophores, and is thus triploblastic. It has no coelom. Most species possess protonephridial tubules and flame cells and some have excretory bladders. The available evidence indicates that these organs are osmoregulatory rather than involved in nitrogen excretion.

A protonephridial system is the characteristic osmoregulatory mechanism of flatworms, nemertine worms and some of the rather heterogeneous group designated as Aschelminthes, as well as the entoprocts, the next four phyla to be discussed. This system consists of varying numbers of tubules closed at one end by specialized cells equipped with long cilia or flagella which keep the fluid contained in the tubules in motion. The cells are called flame cells or solenocytes, depending on criteria which may not be valid but they function in the same way. If the system is fully developed the tubules empty by way of dilated ampullae into a contractile bladder which opens to the outside through an excretory pore.

Although the protonephridial system is more complex than a contractile vacuole and may in some instances have an excretory function, its major function appears to be to get rid of excess water. Water moves into the system of tubules by an active uptake mechanism, is kept in motion by the action of the flame cells, and is expelled to the outside by contraction of the bladder. An osmoregulatory function is indicated by the fact that the system is poorly developed in marine flatworms but is highly developed in freshwater species. On the other hand some marine Turbellaria have flame cells as do the free-living larval stages, the cercariae, of trematode parasites of marine fishes.

Webb, Johannes and Coward (1971) found that both a freshwater and marine starved turbellarian species lost free amino acids from the tissues at a higher rate at higher salinities.

The English turbellarian, *Procerodes ulvae*, lives under stones where streams enter the sea and undergoes changes from sea water to one-tenth sea water during

one tidal cycle. The fresh water of the streams is rich in Ca and CO_3 (Pantin 1931a). In Plymouth tap water the worms swell to double their size, then decrease slightly and in 48 hours they die. In the high calcium waters of their home stream they swell little and calcium added to the tap water protects them (Weil and Pantin 1931). Apparently calcium lowers permeability of the worms to water. In this connection Pantin (1931b) has shown that the worms lose 25% of their salts in dilute solutions while taking in water, and Ca reduces the rate of salt loss.

Beadle (1934) has analyzed the case further and showed that the worms live indefinitely in salinities ranging from full sea water down to 5% sea water. When placed in diluted sea water the worm swells and activity decreases; then the excess water in the swollen parenchyma is taken up by the gut cells, which become vacuolated, and equilibrium is reached with a return of activity. This situation is maintained in the presence of Ca so long as the animal remains in diluted sea water above 5%. At lower dilutions cytolysis occurs.

In *Procerodes* the role of the flame-cell system is in question. Protection against dilution during the two daily tidal cycles is accomplished by a special mechanism involving temporary storage of water in endodermal cells lining the gut, as mentioned above. The vacuoles have not been observed to empty into the gut as might be expected. It is possible that the flame-cell system is involved in some manner as yet unknown.

Rees (1941) observed a European tide pool species, *Monocelis fusca*, that lived at salinities from 26 to 64 ppt. Experimentally it could survive transfer to salinities from 5.6 to 76.8 ppt. If the salinity was gradually raised the worms could survive salinities up to 120.3. They could also secrete mucous cysts in which they withstood sea water evaporated to about 275 ppt.

Kromhout (1943) studied a species, *Gyratrix hermaphroditus*, which has fresh, brackish and sea water populations. He found progressive loss of components of the protonephridial system from fresh water to sea water. In the latter medium the tubules, ampullae and paranephrocytes were all absent.

Various flatworms are enemies of oysters over widely spaced areas of the earth. Stead (1907) observed *Leptoplana australis* killing oysters during dry periods in Australia. Danglade (1919) reported the oyster leech from five areas in Florida. Roughley (1922) observed that freshets killed the "wafers and borers" and were thus beneficial to oysters. Villadolid and Villaluz (1938) reported *Psudoceros* sp. as attacking oysters in the Philippines when the salinity was high.

Pearse and Wharton (1938) found that the predatory oyster "leech" of Florida, *Stylochus frontalis*, laid eggs which developed normally at salinities from 17.8 to sea water and would live experimentally as low as 15.5 ppt when transferred directly. It would not lay eggs at salinities below 15 ppt. The worm died at 6 ppt sea water.

Landers and Toner (1962) transferred *S. ellipticus* from Milford Harbor, Connecticut, to various salinities. They all survived down to 7.5 ppt, but at that salinity they lost color, secreted an abnormal amount of mucous and became sluggish. Worms transferred directly to 5 ppt sea water suffered a 20% mortality and

all died when placed in 2.5 ‰ sea water. Activity and response slowed as salinity decreased below 7.5 ‰ sea water, but worms acclimated to 5 ‰ sea water survived when placed in 2.5 ‰ sea water. Landers and Rhodes (1970) found that lowering the temperatures below 10°C progressively reduced predation but lowering the salinity did not. They also reported that worms from high salinities preferred barnacles as food, but low-salinity worms preferred oysters.

The flatworm phylum is of vast importance biologically because of its parasitic component. However, the free-living species are not numerous in fresh water, sea water or damp earth and thus are not trophically important to the life web. Probably the oyster enemies, *Stylochus frontalis* and *S. ellipticus*, of the eastern and southern seaboard are the most important of all. Presumably they would be killed by sudden influxes of fresh water.

The swimming larval stages of the fluke and tapeworm parasites of the Phylum Platyhelminthes are as exposed to the salinity of the environment as the free-living species, but very little is known of their salinity limitations. Stunkard and Shaw (1931) placed larval trematodes (cercariae) in six mixtures ranging from tap water to pure sea water. The conclusion was that these marine parasites could complete life histories in salinities as low as 4 to 8.5 ppt.

Kawashima and his associates have shown that miracidia of the lung fluke *Paragonimus ohirai* will easily infect three shore snails of the genus *Assiminea* in the laboratory, but in the field are found only in *A. parasitologica* which is found at the high tide line. The snail and miracidia both seem to prefer the low salinities at this tide level rather than the higher salinities at the lower tide levels preferred by the other two snail species (taken from Schwabe and Kilejian 1968).

Styczynska-Jurewick (1971) worked with three marine trematodes from tidal waters and a freshwater species. Cercariae from brackish waters survived over a wide salinity range and the freshwater species survived salinities up to 18 per mille.

Larvae of the liver flukes of cattle and sheep encyst on grasses and plant stems that are sometimes submerged in water. In the marshes of western Louisiana, cattlemen have noticed that their cattle do not get liver flukes when grazing on marshes that have been flooded with brackish waters. Presumably the trematode cysts are killed by the brackish water salinities.

Schwabe and Kilejian (1968) have given a brief review of "osmochemicals" and platyhelminth parasites and the readers who are interested in further details are referred to that account.

G. NEMERTEA. The nemertines are smooth, unsegmented, ribbon-like worms. They are ciliated and have no coelom and some zoologists are impressed with their similarity to the Platyhelminthes. But they have an anus, a circulatory system and a very distinctive eversible proboscis for capturing prey, quite unlike any flatworm. Some of them (*Cerebratulus*) are classical material for embryological work and morphological studies because of their penchant for fragmentation. They are notable as voracious feeders on any organism they can capture with their proboscis which may be covered with an adhesive substance or armed with stylets.

Some of them, *Lineus*, may be 20 meters in length and some are found to depths of over a thousand fathoms in the ocean. A few live in freshwater lakes and streams and even under damp logs, but predominantly they are creatures of the ocean shore and shallows down to about 10 fathoms (see Coe 1954). Some nemerteans have no larva; others have a helmet-like larva called a pilidium or a crawling "larva of Desor."

Coe stated that there were 53 known species on the Atlantic continental coast, 95 on the Pacific and 17 in the Gulf of Mexico. The group is not great in biomass and it is not of great trophic importance. Salinity relationships have not been recorded, to our knowledge, except that all workers have noted that the marine species are mostly found in the lower bays and the outside higher salinity waters.

H. ASCHELMINTHES. This is a grouping of what was formerly considered to be five phyla. The common characteristics are a pseudocoel, lack of segmentation, a covering of cuticle, a straight nonmuscular intestine and a posterior anus. Many members of these groups are given to cell constancy, that is, a given species has a given number of cells. The pseudocoel is the body cavity surrounding the gut, and is the first seen as we go up the scale of increasing complexity of animal organization; but it has no epithelial lining and it derives from the blastocoel of the embryo. Thus it is not a coelom.

The lumping of such different animals into one phylum appears to be a strained classification and it will probably dissolve as more facts are brought to bear. In any case four rather inconsequential types of organisms, the Nematomorpha, Rotifera, Gastrotricha and Kinorhyncha are cast together with the numerous and important Nematoda.

The Nematomorpha superficially resemble long nematodes, but they all possess a cloaca, lack an excretory system and are all parasitic in arthropods. Only one genus *Nectonema* is marine and the group merits no further consideration here.

The Rotifera are denizens of fresh water and the shallow sea. The body has a flat bell-shape with a stemlike foot. There is a trochal disk of cilia around the mouth which has caused the name "wheel animalcule" to be given to these little animals. Females are small and males are minute or absent in many species. Breeding entails a violent piercing of the female body wall to the inner cavity. Most marine species are epizoic, that is, they are creepers on the bodies of larger animals. They are of little ecological importance. Bayly (1967) reported one species, *Brachionus plicatellus*, in a salt lake in New Zealand at 15 ppt with NaCl predominating. The authors know of no other salinity data on the rotifers.

The Gastrotricha are about 1 mm long. They are covered with scales and bristles. An excretory system with two flame cells is sometimes present. Cilia are present on areas of the body. They have a typical constricted area behind the head called the neck. There is a sort of vacuolated series of body spaces called pseudocoels. One order is exclusively marine, but distribution is very spotty and it is known mostly from Europe.

The Kinorhyncha are minute cylindrical animals living usually in shallow marine and brackish water sediments. The body is superficially divided into 13 segments. The head may be retracted into the trunk region leaving the spines

protruding. The sexes are separate. Kinorhynchs are exclusively marine and are widely distributed on muddy bottoms, sometimes in low-salinity water. The salinity relationships of these organisms are otherwise unknown.

Nematoda are elongated round worms, covered with a cuticle and generally rather pointed at each end. They have nerve cords and an excretory system. Muscles within the body only permit a lashing type of movement back and forth and this is the only type of movement these animals have. Some organ systems, especially the nerves, exhibit constancy of cell number.

These worms are enormously abundant, widespread and variable in their ways of life. They vary in length from a millimeter or less to several meters long in some parasites. They are free-living as scavengers or predators or suckers of plant juices and they are parasites in thousands of species of animals and plants. Public health authorities have pointed out that thousands of tons of nematodes exist as parasites inside human beings in backward parts of the Earth. They cause elephantiasis, hookworm and several other diseases in man and domestic animals. One authority stated that if the whole earth except for the nematodes disappeared, its general outlines and features, including buildings, and larger plants and animals would be signified by the remaining nematodes alone.

Nematodes have been around so long and are so numerous in the ground that certain soil fungi have become adapted to very quickly growing a net of filaments around living nematodes and secreting juices which digest them. It has been estimated that the top three inches of sea beach sand contain five billion nematodes per acre and there are more thousands of millions per acre on the ocean bottom (Sprent 1972).

In spite of these well-recognized generalities, the impact of nematodes upon the life web of the sea in terms of trophic and ecological relationships is not known and can only be dimly perceived. The soil forms certainly serve as food for the mud-eaters and the parasites have large effects upon billions of marine organisms, but the details are lacking. Similarly the relationships of nematodes to salinity are almost completely unknown. It may be surmised from the broad distribution of nematodes that they are adaptive or tolerant to wide ranges of salinity, especially the shallow-water or nearshore species.

The cuticle which covers the body is permeable to water entering but not leaving (Meglitsch 1967) so there must be some mechanism for getting rid of excess water in those species which live in fresh and low-salinity waters. They do not have a protonephridial system but rather have a special gland cell, the renette cell, and sometimes tubes derived from it. Neither excretion nor osmoregulation is understood in nematodes but there is evidence that the intestine is the major site of nitrogen excretion. Evidence of changing activity of the excretory system with osmotic stress indicates an osmoregulatory function, but there is uncertainty about the mechanism involved (Meglitsch 1967).

In the middle reaches of the Blyth Estuary at stable marine salinities, it was found by Capstick (1959) that the populations were 3,000 per 100 square cms in sand and 28,800 in thick black mud. The latter figure is equivalent to about 11

billion to the acre. Three transects were made across the intertidal zone from the channel to shore in the lower, middle and upper reaches. Even though the differences of interstitial salinities were small, 21–32 ppt upper and 26–34 ppt lower, there was a considerable salinity effect. Populations decreased upstream and among the 37 species taken the population was primarily of marine origin.

Chitwood (1951) says that true brackish water nematodes are not known and that the transition from fresh water to marine species is a "quick change."

Timm (1952) reported 78 species from the Maryland (upper) portion of Chesapeake Bay at salinities ranging from 8 to 16.9. Some species were known before from fresh water, but most were marine.

Tietjen and Lee (1972) found the generation time of *Monohystera denticulata* was 10–12 days at 25°C and a salinity of 26 ppt, which appears to be the worm's optimum for both factors. The variation of salinity in either direction increases the generation time.

Attempts to acclimate marine nematodes to fresh water and *vice versa* have failed (Chitwood and Timm 1954), but a Massachusetts species found in decaying seaweed, which has been cultured on agar made up from tap water or sea water, later could be transferred directly to either medium. Those authors also noted that the excretory system is much better developed in freshwater nematodes than in marine species. They suggest that a study of estuarine forms would be interesting, because there is practically no overlapping of freshwater and marine species.

I. ACANTHOCEPHALA. This is a small phylum of spiny-headed parasitic worms. It has no digestive tract and usually no excretory system. The proboscis is armed with hooks and it invaginates. Sexes are separate. All species are found in the vertebrate digestive tract and there are no free-living stages. Thus they are limited to salinities their hosts can tolerate. Several species are found in marine birds and fishes. Their salinity problems are essentially those of their hosts, but parasites are in a sense buffered by their hosts, and in a sense the Acanthocephala have no osmoregulatory problems, or if they do they are not known.

J. ENTOPROCTA. This is a small phylum of small, sessile animals formerly included with the Bryozoa. Except for one fresh water genus, *Umatella*, all of them live in the sea. They have a pseudocoel and all of them have flame-cell protonephridia. To what degree these function in excretion or in osmoregulation has not been determined. The organisms consist essentially of a goblet-shaped calyx, containing the viscera, on a supporting stalk. The calyx is mounted by a ring of ciliated tentacles. The mouth and anus open within this ring. In most species the stalks produce stolons which branch and produce other stalks and calices and thus a colony. A second group is solitary and lives commensally with sponges, tubeworms, and bryozoan colonies and other invertebrates.

The Entoprocta are not of much trophic consequence and their salinity relationships are unknown.

K. ANNELIDA. The segmented worms comprise a very important phylum with a true coelom, a linear grouping of segments separated by septa and very much

alike with regard to nerve and blood vessel branching and the replicated nephridial system. The animals are dioecious or bisexual but cross-fertilization occurs in the latter. There are three large classes and a small one.

Annelids have successfully populated fresh, brackish, and salt water as well as damp terrestrial environments. The characteristic excretory structures of this group are the metanephridia which are involved not only in excretion of nitrogenous wastes but also in water and electrolyte balance. Metanephridia differ from protonephridia chiefly in that instead of ending blindly in closed cells, they open by way of ciliated funnels called nephrostomes into the coelom. The nephrostomes continue as tubules or canals of varying complexities which eventually open to the outside through nephridiopores. In some of the more primitive worms protonephridia may still be present, and in some cases the tubules may be reduced to simple sacs. Coelomic fluid can pass into the nephrostome and as it passes through the nephridial canal various components including water and salts may be reabsorbed. Thus the excretory system may be involved in osmoregulation and in ionic regulation.

The Archiannelida is made up of a small number of marine, brackish or fresh-water species, most of which are to be found in the interstitial water of sand. They are heterogeneous and are united for convenience only. Simplification of anatomy is mostly due to small size and the group is not primitive. The trophic importance of the group is small and its salinity relationships are unknown.

The Oligochaeta is a group of largely freshwater or terrestrial worms of which about half are earthworms. They have setae on each segment, but no parapodia. They have no eyes. Some freshwater species are sometimes secondarily littoral-marine. Very few are to be found in sea water and salinity relationships are not well known.

Jansson (1962) showed that an interstitial oligochaete, *Aktedrilus*, from 6 ppt tolerated 1.25–20.0 ppt, but preferred 2.5–5 ppt and preferred 5 ppt even after 8 days at 20 ppt. Another species, *Marionina*, from 2 ppt tolerated 2.5–10 ppt for 6 days. The same species from zero salinity preferred 0.2–0.3 ppt.

Kahler (1970) showed that acclimation of the oligochaete, *Enchytraeus*, to high salinity increased its resistance to temperature extremes. The effect decreases with rising adaptation temperature.

Lassere (1970) has shown that two euryhaline oligochaetes take up salt at 3–25 and 3–30 ppt. Outside these limits the variation in oxygen intake indicated a metabolic disturbance.

Zoology texts generally state that earthworms are terrestrial. However, marine earthworms are found on the island of Bermuda and in Redfish Bay in South Texas. The senior author has taken the latter in lenses of water, with a salinity of 34.0 ppt, over coarse sand and always under piles of rotting seaweed. Apparently the worms do not dig into the sand and do not ingest it.

Studies of the earthworms *Lumbricus terrestris* (Ramsay 1949) and *Pheretima posthuma* (Bahl 1947) which live in contact with soil water and can live in aerated fresh water indicate that, in fresh and brackish water, salts are absorbed by the

nephridia resulting in production of a hypotonic urine. Krogh's work (1939) showed a similar mechanism for leeches.

The Hirudinea are predaceous worms or blood-sucking ectoparasites. A number of species are marine but the greatest number are found in fresh water. They have many features in common with the oligochaetes, but all species known have 33 segments, a constancy not found in any other annelid group. Salinity relationships are virtually unknown.

Ramamurthi (1968) has shown that an Indian cattle leech can be acclimated to 38% sea water and some survival was obtained at 75% sea water. The leeches had minimum oxygen consumption at 25% sea water and a maximum at 50%. They were isotonic at 25%. The fact that these essentially freshwater animals can be acclimated to low percentages of sea water is not surprising when we consider that their food, vertebrate blood, ranges from about 12 to 14 ppt saline.

Most of the studies of osmoregulation in annelids have been done with members of the class Polychaeta, particularly with the nereids, which include both brackish and marine species as well as a few that can tolerate fresh water. Some work has been done with the lugworm *Arenicola marina* (Schlieper 1929, Wells and Ledingham 1940) and with a few other polychaetes.

Dice (1969) took specimens of California species, *Cirriformia spirabrancha*, from sea water and placed them in a series from zero to 300% sea water; at 150% shrinking occurred; at higher salinities movement decreased and swelling took place. Duchâteau-Bosson, Florkin and Jeuniaux (1961) found that loss of amino acids in *Arenicola* transferred from sea water to half sea water accounted for 41% of the osmotic pressure change. Ebbs and Staiger (1965) reported *Onuphis magna* as a hyperosmotic regulator at less than 15 g/l chloride. Under hypersaline conditions there is swelling followed by volume regulation. The first 10 to 15 segments, which have no nephridia, swelled most. Ellis (1939) found that *Nereis diversicolor* is able to regulate in brackish water, while *Perinereis cultrifera*, a stenohaline species, cannot. The first species lost salt and swelled least. Fretter (1955) found that the integument of the latter species is much more permeable to ions than *Nereis*, which takes up sodium, nevertheless, over a wide salinity range. Jeuniaux, Duchâteau-Bosson and Florkin (1961) report that both in *N. diversicolor* and *P. cultrifera* osmoregulatory mechanisms involve amino acids. The first species is more euryhaline than the latter. Losovskaya (1961) studied three Black Sea species. He reported that *N. zonata* withstood a salinity fluctuation from 10–30 ppt. There was a 3% mortality at 40–45 ppt. The optimum for *Platynereis dumerilii* was 15–30 ppt at 20–24°C. *Melinna palmata* had an optimum of 9–30 ppt salinity at 9–21°C. Pearse (1928) worked on four American Atlantic species: *Nereis virens*, *Scolecolepides viridis*, *Arabella opalina*, and *Glycera dibranchiata*. The first showed considerable tolerance for one-fourth sea water and the second two did well for several days at half sea water and all tolerated three-fourths sea water. At low salinities all of them showed a tendency to swell, become turgid and extended. Robertson (1949) studied several marine invertebrates in Scotland, including the polychaetes, *Arenicola* and *Aphrodite*. He found that they regulate potassium and sulphate, and in ionic ratios were similar to the jellyfish and echinoderms in contrast to the higher

crustaceans. Smith (1953) found that the Pacific species, *Nereis lighti*, lived at 2-3% sea water in the upper Salinas Estuary and near the river mouth at 40 to 100% sea water, both locales being more favorable than the lower estuary which has full tidal exchange part of the year. Smith (1964a) found that *Nereis succinea* in 50% sea water loses salt at a much higher rate than *N. limnicola*. Both worms show equal water intakes at given wet weights. No increase of water intake with increased osmotic gradient was shown.

The class Polychaeta includes osmoconformers and osmoregulators of varying efficiencies. *N. pelagica* (Schlieper 1929) and *N. vexillosa* (Smith 1963, Oglesby 1965) and *Perinereis cultrifera* (Beadle 1931, Ellis 1939, Wells and Ledingham 1940) are stenohaline conformers. *Cirriformia spirabranchia* (Dice 1969) can hyperregulate to some degree but its lowest salinity tolerance is higher than that of the nonregulating *Arenicola marina* which is able to tolerate wide ranges in internal concentration.

Laeonereis culveri (Oglesby 1965), *Nereis succinea*, *N. limnicola* (Smith 1963, 1964a; Oglesby 1966), *N. virens* (Potts and Parry 1964a), and *N. diversicolor* (Schlieper 1929, Beadle 1937, Ellis 1937) conform at high salinities and hyperregulate at low salinities, but they vary in their lower salinity limits. According to Beadle the worms use more O_2 at lower concentrations not because of osmotic work but because muscles contract to counteract swelling.

The euryhaline species *N. diversicolor* has received considerable attention. When it is first subjected to a dilute medium it swells due to osmotic intake of water at a faster rate than can be handled by the excretory system. However, as the body fluids become more dilute and there is less gradient between internal and external concentrations, water intake is reduced. Calcium in the dilute environmental water aids in this reduction by reducing permeability. When water intake is sufficiently reduced it is exceeded by water excretion and by actual expression through the nephridia and swelling subsides (Beadle 1937, Ellis 1937).

Initial rapid loss of salts also contributes to reduction of the internal concentration and restriction of swelling. Although the body fluids are diluted, they remain more concentrated than the environmental water and hyperosmoticity is maintained. In spite of an initial rapid salt loss, in the latter stages of adaptation salt is actively absorbed, possibly under stimulation of a lowered blood concentration. Maintenance of hyperosmoticity has been thought also to require reabsorption of salts by the nephridia and excretion of a hypotonic urine (Ellis 1937). The complexity of the nephridium as compared with other species suggests such a function. It is long and coiled and could provide a large surface area for reabsorption. The nephridium of the conformer *Perinereis cultrifera* is a simple sac (Brown and Stein 1960). Potts and Parry (1964a) believe, however, that active uptake is sufficient to balance loss of salts by diffusion and in the urine except at very low salinities. There is little doubt that *N. diversicolor* actively osmoregulates since the ability to maintain hyperosmoticity is lost in the presence of cyanide or in the absence of oxygen.

Other factors may also be involved in adaptation of this species to low salinities. Comparative studies have shown that in dilute media *N. diversicolor* is less

permeable to water and ions than other nereids tested. *N. pelagica* and *N. virens* are about three times as permeable to water as *N. diversicolor* (Jørgensen and Dales 1957). *N. virens* can hyperregulate but because of more rapid water uptake it must exert more energy to do so and it cannot tolerate as low salinities as *N. diversicolor* (Potts and Parry 1964a). *P. cultrifera* is about three times as permeable to sodium (Fretter 1955) and *N. virens* is about three times as permeable to chloride (Jørgensen and Dales 1957) as *N. diversicolor*.

N. diversicolor may also live successfully in dilute media because of tolerance of its tissues to dilution. In spite of low permeability as compared with other species and some osmoregulatory ability, dilution of its body fluids does occur at low salinities. Wells and Ledingham (1940) showed that isolated muscles of *N. diversicolor* function normally in salinities as low as 5% and 10% sea water, whereas those of the stenohaline *N. pelagica* do not function in salinities lower than 20% sea water.

There are some differences in the various populations of *N. diversicolor*. Smith (1955b) found the lower limit to be 4 ppt in Finland, and 1.25 in Denmark. Smith (1955c) compared the blood and media of worms from four European regions ranging from an upper limit of 2 ppt to stable high salinities. The worm was found to be a typical adjustor above about 10 ppt salinity and was a regulator in lower salinities. Smith (1955a) found, that in sand, lowered salinities of 9–29 ppt persisted even at high tide. *N. diversicolor* was found there in greatest abundance. Smith (1956a) found no significant differences in chloride regulation of populations of *N. diversicolor* from widely distributed and different habitats and salinities. Smith (1956b) found this species regularly endures salinities of 0.5 in the Tamar River Estuary and is not found in true marine situations. Smith (1964b) found that larval development of *N. diversicolor* in Finnish waters at salinity from 5.4–6.3 ppt took place at 3 to 10g Cl/l, with an optimum of 7.5; Swedish worms from a salinity of 20 ppt developed at 5–15g Cl/l with slower rates near the extremes.

In summary, *N. diversicolor* exhibits at least four characteristics that contribute to its euryhalinity: (1) relatively low permeability to water and ions, (2) volume regulation, (3) active uptake and possible reabsorption of salts by the nephridia and (4) tolerance of tissues to dilution of the body fluids.

Tolerance to changes in internal concentration is a characteristic of estuarine species. Other than certain behavioral patterns, it is essentially the only way that conformers can cope with changing osmotic conditions, and many regulators also tolerate considerable variation in body fluids. Tissue tolerance involves osmoregulation on a cellular level, yet intracellular water and salt composition must be held relatively constant. Experimental evidence indicates that cellular osmoregulation is accomplished largely by changes in concentration of free amino acids in the cells. The kinds of amino acids involved vary with the species, but in a number of animals tested the total concentration varies directly with variations in concentration of the body fluids.

Studies have been made of variations in tissue composition of some annelids as related to salinity changes. At high salinities the muscles of the conformer *Arenicola marina* contain higher levels of amino acids than at low salinities, with

glycine and alanine showing the greatest change (Duchâteau-Bosson, Florkin and Jeuniaux 1961). *Perinereis cultrifera*, which cannot regulate blood concentration, shows changes in amino acids with changes in salinity that are larger than those exhibited by *N. diversicolor* which exhibits some degree of osmoregulation (Jeuniaux, Duchâteau-Bosson and Florkin 1961).

Some studies have been made purely of distributions. Amos (1957) found *N. succinea* at 8.8 to 30.7 ppt in Delaware Bay and most abundant at 20–21 ppt. Estcourt (1967) gave the distribution of 15 species over a salinity gradient in Heathcote Estuary, New Zealand. Only two species were found where salinities dropped down to fresh water. Hempel (1957) compared *Polydora ligni*, which is found at up to 80 ppt in the Laguna Madre, with *Pygospio elegans* found at 2.1 ppt in the Baltic-North Sea Canal. Hill (1967) found *Ficopomatus* in Nigeria only above 33 ppt, while a serpulid *Hydroides uncinata* only lived between 20 to 30 ppt; another serpulid lived from 0.5 to 18 ppt, but not at 21. Loosanoff and Engle (1943) reported that *Polydora websteri*, a commensal of oysters which sometimes riddles their shells with its tubular excavations, does not grow well at salinities above 25 ppt. Muus (1967) reports a morphological cline of *N. diversicolor* from Finland (low salinity) to the North Sea (high salinity).

A few workers have studied the effects of salinity on the development of annelids. Berger and Lebskii (1969) found if fertilized eggs of *Evilia viridis* were transferred from 25 ppt to 14 ppt and below they died immediately. At 16 ppt three divisions took place and at 18 division went on to 64–128 blastomeres. Trochophores were formed only at the normal salinity 20–24 ppt. Similarly they found that the life cycle of spermatozooids increased from 16 ppt and reached a maximum at 20–25 ppt. Klesch (1970) found *L. culveri* at salinity variations of 2–64 ppt. Spawning took place at 44 ppt. The highest density of worms, 203 m², was at 28 ppt. Lyster (1955) put *Phyllodoce maculata* larvae in a vertical salinity gradient and found that the larvae congregated at about 12 ppt because they could not swim higher in the fresher water of lower specific gravity. It was said that this prevented the worms from being carried out of the estuary as the low-salinity water flowed out at the surface. Mohammad (1966) found that 16 ppt was fatal to the eggs of *Axiothella mucosa*. Larvae and juveniles raised at optimum salinities, 32–40 ppt, showed swelling at 16 ppt but readjusted after one week. Low temperature and low salinity acted independently in slowing growth.

A recent study by Oglesby (1973) has shown the lugworm *Abarenicola pacifica* is an osmotic conformer within the limits of its tolerance, which is as low as 23% sea water in the laboratory, but the coelomic fluid is slightly hyperosmotic to the medium. A literature review shows this to be characteristic of other members of the family. In contrast, the coelomic fluids are slightly hypo-ionic to the medium in chloride and sodium. The animal has very little ability to control its volume and water content at different salinities. It is concluded that this lugworm will not form permanent populations where the interstitial salinities fall below 50% sea water.

Many polychaete worms live quite successfully in an estuarine environment. Like other species they have developed more than one method of coping with fluctuating osmotic conditions. Some, like *Arenicola*, conform, regulating only at the cellular level, while others, like *N. diversicolor*, maintain hyperosmoticity by

active transport mechanisms. Some swim away and some withdraw into tubes or holes.

It is clear that the various marine worms are considerably affected by salinity and have developed several ways of coping with it. As the salinity changes in an estuary large changes in the marine worm population will take place, but the details are not well known.

L. ECHIURIDA. This is a small group of worms that mostly burrow in the sand and mud of shallow waters, but have been taken from 4500 fathoms. These worms seem to have affinities with both the annelids and the next group, the Sipunculida, which are unsegmented. They have a trophophore larvae like the annelids, but metamorphism is only transitory in development stages. The group is not ecologically important and there are only scattered records from the Gulf of Mexico (Hedgpeth 1954a).

M. SIPUNCULIDA. This is a group of unsegmented worms with a trophophore larvae. There is no circulatory system. They are found in sand or mud to 3000 fathoms. They are small and not numerous and, for instance, there are only 11 species from the Gulf of Mexico, with only one known from the northern Gulf and 10 from South Florida (Hedgpeth 1954a). They are detritus feeders chiefly. The group is of little ecological importance and there is little information on its salinity relationships. Hogue and Oglesby (1972) studied the osmotic and ionic concentrations of *Themiste dyscritum*, a large Pacific coast species acclimated to 41–101% sea water. Oglesby (1969) reviewed the literature. He concludes that all sipunculids studied are osmoconformers at all tolerable salinities, with weak powers of ionic regulation at any salinity.

N. PRIAPULIDA. This is a small group of worms living in the mud of temperate seas down to 44 fathoms. This group has recently been found to be coelomate. The surface is superficially segmented. The mouth and pharynx are eversible. There is a peculiar larva within a case or lorica. The animals are predaceous and feed in part on annelid worms. They are sublittoral and not often subjected to salinity changes.

O. MOLLUSCA. It is customary in most zoological classifications to follow the Annelida with the Arthropoda, to which they are thought to be so similar, chiefly because of metamorphism. But they seem to be a much higher group than the molluscs in diversity as a whole and in complexity of parts, in spite of the fact that the octopus is said to have the finest brain outside of the vertebrates. Furthermore, the arthropod larvae have no resemblance at all to the annelid trophophore and the Arthropoda have no cilia at any stage. The molluscs are replete with cilia and their early veliger larva is a sort of prototroch. Lastly, the Mollusca arose as early as the Arthropoda in the geological time scale. Fossil gastropods and bivalves are known from the lower Cambrian along with the trilobites.

The Mollusca rank next to the arthropods in numbers, but except for one group of gastropods, they have not invaded the land.

The Monoplacophora is a primitive group recently found in bottom trenches

off western America and in the Gulf of Aden. It shows indubitable seriation of parts or metamerism, indicating kinship to the Annelida. Fossils are known from the early Cambrian. This remnant group comes from high-salinity and generally deep waters and is not subject to salinity modification.

The Amphineura include the shellless, wormlike solenogastres and the chitons with eight hinged shells on the back. They are combined chiefly because of the primitive nervous system. The chitons live mostly in the littoral and sublittoral of rocky shores. The solenogastres burrow in mud, sometimes at great depths, or crawl over soft sessile animals on which they feed. This class of molluscs is not numerous or well-studied and salinity relationships have not been recorded.

The class Scaphopoda is an elongated tooth-shaped group of molluscs that burrow in sand and mud and are reported to feed mostly on Foraminifera. They are a small group and salinity relations are unknown. They are not estuarine.

The Cephalopoda are the squids, cuttlefish and octopuses. They are considered to be purely marine. Out of 276 short squids, *Lolliguncula brevis*, taken over a two-year period, Gunter (1950) collected 97 in Aransas Bay, Texas, and the remainder in the Gulf. The salinity range was 17.7–37.2 per mille. Forty-eight squid were caught at less than 25 ppt and nine were taken below 20. The size of the squid in saltier water was greater than at lower salinities. Gunter (1950) also took 45 *Loligo pealeii* in offshore waters at salinities from 30.7 to 35.8 per mille. He reported small octopus, *Octopus vulgaris*, from bay waters but had no salinity data. Cephalopoda of some species do venture rarely into waters of median salinities in estuaries.

The Gastropoda are predominantly marine snails and there are about 40,000 known species. A characteristic twisting and coiling has been superimposed on bilateral symmetry resulting in a single coiled shell. The Prosobranchia have a head and tentacles and sometimes eyes, and a shell closed by an operculum. They are scavengers or predators and sometimes bore holes in their prey with a radula or kill them with poisons. Many small species scrape unicellular organisms from rocks for a living. This is the main group of gastropods in the bays and estuaries. The Opisthobranchia are species with shells reduced or absent such as the sea hares and pteropods. They are fully marine and many are planktonic on the high seas. Relatively few come into low-salinity waters. The Pulmonata are similarly found in small numbers in estuaries, being mostly land snails.

The Pelecypoda or Bivalvia have a poorly developed head, consisting of a mouth at the end of the visceral mass. They have close-fitting bivalves for protection. This is the only class of the Mollusca without a radula. They are plankton or detritus feeders and are sometimes dominant organisms in bays and sounds.

In the following account all groups are treated together:

The mechanisms involved in osmotic and ionic regulation in molluscs are the same as already described for other invertebrates. In general they do not hyperregulate as well as crustaceans, possibly due to the greater permeability of their soft bodies, but many have the advantage of being able to close their shells tightly and maintain an immediate environment quite different in concentration from the outside water. Milne (1940) showed that the euryhaline mussel *Mytilus edulis* can maintain

a salinity of 24 ‰ within the mantle cavity when the outside water has a salinity as low as 7 ‰. Pearse and Gunter (1957) noted that oysters very often taste salty when the surrounding water may be practically fresh. Shelled molluscs can remain closed for relatively long periods but must eventually open to feed. Therefore, all euryhaline, brackish, and fresh water species must make adjustments to low salinities.

Species subjected to varying salinities appear to rely almost altogether on cellular regulation. They exhibit little ability to regulate blood concentration but can tolerate wide internal variation. *Mytilus edulis* occurs in salinities ranging from 30 ‰ to as low as 4 ‰ (Segerstråle 1957) and is isosmotic to all salinities at least above 10 ‰. Conklin and Krogh (1938) reported that specimens from 5.5 ‰ were isosmotic, but Beliaev and Tschugunova (1952) reported slight hyperosmoticity at 4 ‰. Beudant (1816, *vide* Robertson 1964) claimed to have acclimatized this species to fresh water by gradual dilution of sea water over a period of 5 to 8 months. In any case, measurements of blood concentration have shown that it can vary from a freezing point depression of 0.58, or about 10 ‰, to 2.2, or about 38 ‰ (Potts 1954b). Isolated tissues function normally in 40% to 150% sea water (Pilgrim 1953).

On the coasts of the United States the mussel *Brachidontes exustus* is found in high-salinity areas of estuaries and *B. recurvus* is found in low salinities. However, this species is more susceptible than oysters to being killed by freshets because the closed shell leaks through the byssus opening.

Castagna and Chanley (1973) studied salinity tolerance of 36 species of common bivalves from Virginia estuarine waters by distribution and tolerance studies in the laboratory. Most of them were tolerant of wide variations, but one-third of the species were not found in nature over the whole range of salinity they were known to tolerate, because temperature or other environmental factors were overriding.

Most brackish water molluscs are conformers, but a few hyperregulate at salinities below 50%. Hyperosmoticity has been demonstrated in the snail *Littorina littorea* at salinities below 17 ‰, but this species is isosmotic at higher salinities (Todd 1964a). The gastropods *Hydrobia ulvae* and *Potamopyrgus jenkinsi*, which have invaded fresh water in recent times, also hyperregulate to some degree (Todd 1964b).

All fresh water molluscs are hyperosmotic, but their body fluids may be more dilute than that of most conformers. The fresh water clam, *Anodonta cygnea*, has a blood concentration equivalent to about 3 ‰ sea water, the lowest of any known animal (Potts 1954a). Its lack of ability to maintain a higher blood concentration may be related to its large gill area and low metabolic rate. Fresh water molluscs maintain hyperosmoticity by the usual method of taking up salts to offset their loss by diffusion and in the urine. The excretory organs, which in the molluscs open from the reduced coelom represented by the pericardial cavity, are involved in osmoregulation and ionic regulation. A large volume of hypotonic urine is excreted. Comparison of the kidneys of certain fresh and brackish water populations of the same species shows correlation with habitat. The kidneys of fresh water populations of *Lymnaea peregra* are larger than those of brackish water populations (Hubendick 1948). This species has the highest known blood concentration of any mollusc

occurring in fresh water. It excretes a hypotonic urine only 70% of the concentration of the blood (Potts and Parry 1964a).

Marine molluscs are isosmotic but can regulate ions. Gastropods and pelecypods regulate mostly potassium and calcium, but cephalopods regulate almost every ion in the blood. Ionic regulation is accomplished by active uptake of salts and, in the cephalopods at least, by differential excretion of ions by the kidneys (Robertson 1949, 1953). Some soft-bodied molluscs can withstand slight dilutions of the medium by means of volume control. The sea hare, *Aplysia*, swells when first placed in dilute water but, like the polychaete *Nereis diversicolor*, is permeable to salts as well as water and so regains volume and a new steady state with lowered blood concentration (Bethe 1930).

Much recent work has been directed toward elucidating the role of free amino acids and other intracellular organic substances in cellular regulation. There is much indirect evidence of their function. Their concentration is greater in marine invertebrates than in fresh water or terrestrial species. Included among molluscs in which free amino acids have been demonstrated to decrease with decreasing salinities and increase with increasing salinities are *M. edulis* (Potts 1958, Lange 1963, Bricteaux-Gregoire et al. 1964), *Rangia cuneata* (Allen 1961), *Hydrobia ulvae* (Negus 1968), and *Crassostrea virginica* (Lynch and Wood 1966). Knight (1966) demonstrated similar increase in ninhydrin-reactive substances with increased salinities in *C. virginica*. The principal amino acids involved appear to be glycine, alanine, aspartic acid and glutamic acid (Allen 1961). Taurine occurs in relatively high concentrations in many marine and brackish water species, including molluscs, but is absent from fresh water species (Simpson et al. 1959). Its function is not known, but its distribution according to species habitat suggests an osmoregulatory role.

Although *Mytilus edulis* has a very wide salinity range, individuals are small in both high and very low salinities indicating that salinities which approach the upper and lower tolerance limits may represent stress conditions. The same relationship of salinity and size was noted by Andrews (1940) for the snail *Neritina virginea* and may be general. The effect varies with the optimum salinity of the particular species. Although *Mytilus* and *Neritina* are smaller at low salinities, *R. cuneata* is larger (Ladd 1951). Presumably low salinity represents optimum conditions for *R. cuneata*, whereas the optimum for *Mytilus* and *Neritina* is at some intermediate salinity.

Prosser (1964) has stated that there are commonly three periods to be recognized in physiological adaptation as measured by rate functions. First there is shock reaction, second, a stabilized rate for minutes or hours and third, acclimation or compensation over days or weeks. Van Winkle (1972) says these periods are quite evident in ciliary activity and oxygen consumption of gill tissue of four common bivalves (*Crassostrea*, *Mercenaria*, *Modiolus* and *Mytilus*) when subjected to salinity change. He found a shift of recovery time response towards lower salinities for all low salinity acclimated individuals except in *Mercenaria*. There was a correlation between ciliary activity and activity of the whole animal. At low salinity ciliary action decreased, but oxygen consumption increased.

The senior author has shown in several papers cited at the end of this account that among many motile estuarine organisms the young have a greater predilection

for low salinity waters than the larger sizes and the adults. This is demonstrated very clearly in *Thais haemastoma*, the Gulf oyster borer. St. Amant (1938) has shown that in Louisiana the adults come into the bays to where the salinity is around 15 to 18 ppt and he has named this general region the conch line. It amounts to a demarcation because the large *Thais* break off abruptly and do not venture farther up the bays. However, small conchs only a few millimeters long and apparently only recently transformed from the larvae, are found a great deal farther inland at much lower salinities, the lower limit of which has not been determined. The senior author has observed this phenomenon in Louisiana but has not specifically reported it. Similar observations have been reported by Dr. J. G. Mackin in personal conversations.

Although the number of species of typically estuarine molluscs is few compared with marine species, they may occur in vast numbers. Examples are the oyster, *C. virginica*, and the clam, *R. cuneata*. Such species are tolerant of wide internal variation but they can survive extreme conditions only by closing their shells. They can withstand rather long periods of unfavorable environment in this manner. *Rangia* can stand at least seven months in salinity below 0.3 ppt. *C. virginica*, which has a lower salinity limit of about 3 ‰, can survive fresh water at low temperatures for two weeks with its shell tightly closed (Pearse and Gunter 1957). The shell cannot be closed indefinitely, however, so serves only as limited protection against unusual or short-term adverse conditions. If the condition continues, such as in extended floods, death results. Oyster reefs have been completely destroyed by severe floods in the estuarine area of the Mississippi River (see Gunter 1950, 1952). Along with the oysters, commensals such as polychaete worms, barnacles and various small crabs which use the oysters as substrate and hiding places may also be killed.

Changes in which there is an unusual increase in salinity, such as might be produced by prolonged drought, can also be extremely harmful. Oysters can readily tolerate salinities up to full sea water, but increased salinities allow certain predators to move in. The oyster drills *Thais* on the Gulf coast and *Urosalpinx* on the Atlantic coast are particularly devastating. Since these gastropods have a lower salinity limit of 8 to 10 ‰ sea water, oysters in low salinities are protected from them, but during periods of increased salinity they can become established in the beds. Other harmful organisms that become more prevalent at high salinities are the stone crab, *Menippe mercenaria*, the boring clam, *Martesia*, the boring sponge, *Cliona*, the mud worm, *Polydora*, and the flatworm, *Stylochus* (Gunter 1955). Periods of high salinity coupled with high temperatures may result in mass mortality from the fungus *Labyrinthomyxa marinum* (Mackin 1951). It has been estimated that this fungus is responsible for 50% to 60% of oyster mortality during such periods.

A complete treatment of an organism and its relation to salinity is given in the paper by Hopkins, Anderson and Horvath (1973) on the brackish water clam, *R. cuneata*. They studied not only the osmoregulation of the organism as it relates both to amino acids and electrolytes, but they reviewed all the known literature on salinity distributions. They also considered the ecology and life history of this clam as it relates to salinity and to other organisms.

They found that the clam usually lives where the salinity is 1.15 ppt, but that

they could live in the laboratory at 32 ppt for months. The salinities had to change to induce spawning and the larvae only survived at 2–10 ppt saline. They found that where salinities were too stable, apparently recruitment did not take place. The chief importance of this work seems to be the discovery that *Rangia* requires a changing salinity for its existence and that stabilization at any level will eventually wipe out the population. This is ecologically important because this clam, according to the authors, makes up 99% of the bottom biomass in the very low-salinity waters of the Atlantic coast and Gulf bays from Chesapeake Bay southward.

The marsh clam *Polymesoda caroliniana* is found to the landward of *R. cuneata* and sometimes is found in pure fresh water.

P. ARTHROPODA. The Arthropoda are the most numerous and the most diversified of all the animals that live on the face of the Earth and they vary from the primitive horseshoe crab, *Limulus*, which does not even have jaws, but triturates its food with the bases of its forelegs, to the highly organized, socialized insects that are so important on land. As Berry (1929) has said, they are the most abundant forms in the oldest fossiliferous rocks (Cambrian), in the modern seas, and on the land and in the air. All groups including the insects and Arachnida are represented in the sea, except for the centipedes and millipedes. There are no truly marine spiders, but there is an insect, a water strider, on the high seas, and there is a water boatman quite common in the plankton of the open Gulf of Mexico (Gunter and Christmas 1959). There are many species of mites in the shallow sea, but practically nothing is known about them.

All arthropods are members of the protostomia and they have spiral cleavage. They are united by a type of segmentation, which is highly modified in some instances, and by jointed appendages.

The chief aquatic arthropods are the crustaceans. They have invaded fresh water and even land, but they are far and away the dominant animals in the sea and they have been referred to as the "insects of the sea." However, they are more diversified than the insects. Basically the predominant larva is the nauplius which is nothing at all like the modified trochophores of practically all the other protostomia from the flatworms to the brachiopods. For that matter neither is the nauplius similar in any manner to the grubs of the insects.

In this section we shall treat the crustaceans. There are now hundreds of papers and possibly a few thousand which refer to some extent to the salinity relationship of the crustaceans and here we have only summarized the essential features as we recognize them.

Aquatic crustaceans, especially the larger Decapoda, (crabs, shrimp, lobsters, marine crawfishes and the like) have a well-developed circulatory system and heart, plus certain sinuses containing body fluids. They are generally covered with a hard integument, but segments are joined by thinner chitinous membranes and the gills are always exposed directly to the water. The animals are not generally covered by slime as some of the fishes and molluscs are.

Among the invertebrates the crustaceans have developed the greatest powers of osmoregulation. Their hard exoskeletons reduce their permeability to some

extent, but marine species are quite permeable. Their permeability poses no osmotic problem, however, since like marine invertebrates in general they are in osmotic balance, though not in ionic balance, with sea water. The strictly marine species show no osmoregulatory ability and when placed in dilute media below about 70% sea water most of them will swell and die, since they cannot regulate volume nor tolerate dilution of the body fluids (Lockwood 1967). In their natural environment the permeability of marine species to water may be an advantage since water is required for production of the urine involved in ionic regulation, which is exhibited by all species that have been studied.

Some crustaceans are euryhaline, inhabiting both the sea and low salinity waters. A number live in estuarine waters subject to wide fluctuations in salinity. Some species have adapted to fresh water and a few are able to live in hypersaline waters. Permeability seems to be directly related to habitat. Brackish water species are less permeable than marine species and freshwater species least of all (Gross 1957), yet none are completely impermeable. Exchange of water and salts can occur as a result of gradients between internal and external fluids.

The larger, motile crustaceans can respond to salinity changes by actively moving from place to place, and barnacles can close their shells against unfavorable conditions; but most species must adjust to fluctuating osmotic conditions either by tolerating wide changes in blood concentration or by holding such changes to a minimum. Although they vary in their capacities, most euryhaline crustaceans are able to maintain hyperosmoticity at low salinities. They are generally isosmotic at high salinities, but a few species such as the prawn *Palaeomonetes varians* (Panikkar 1941), the brine shrimp *Artemia salina* (Croghan 1958), and the shrimp *Macrobrachium equidens* (Denne 1968) can hyporegulate. The same factors are involved in determining salinity tolerance and osmoregulatory ability in crustaceans as have been described for polychaete worms, that is, degree of permeability, degree of toleration to internal changes in concentration, degree of development of active transport mechanisms, and activity of the excretory organs.

If only passive exchanges were in operation, the blood of brackish and freshwater crustaceans would become intolerably dilute. Instead, it is maintained at hyperosmoticity by active uptake of salts. The few species that can hyporegulate do so presumably by taking in sea water and excreting salts. Even though many crustaceans can maintain a concentration gradient between blood and medium, none can maintain a constant internal concentration at all salinities, although a few can approach it (Panikkar 1941, Croghan 1958). Maintenance of such a condition requires expenditures of energy since on either side of the isosmotic point increasing amounts of energy are required to move salts against greater and greater concentration gradients. It is conserving of energy if the animal, though remaining hyperosmotic or hypo-osmotic, can tolerate some changes in blood concentration which parallel changes in the external medium, thus reducing the gradient between the two fluids. Nearly all euryhaline crustaceans exhibit an osmoregulatory pattern in which the concentration of the blood falls as the concentration of the medium decreases, and rises as the concentration of the medium increases. This method of reducing osmotic work requires tolerance to some degree of internal change.

Tolerance to changes in blood concentration implies that there is osmoregula-

tion at the cellular level. Croghan (*vide* Lockwood 1967) has made some interesting calculations in which he shows that even if the cells could tolerate swelling, a 50% drop in blood concentration would result in total withdrawal of the circulating blood into the cells, assuming a hypothetical animal in which the blood volume constitutes 50% of the total volume. It is obvious that cellular regulation of some sort is necessary for maintenance of blood volume as well as for maintenance of proper cell volume and composition.

Thus, estuarine crustaceans must regulate at both the blood-medium boundary and at the cell-blood boundary. In addition, there must be mechanisms for varying both types of osmotic processes to meet the demands of a fluctuating environment. Regulation at the blood-medium boundary involves active transport of inorganic salts against a concentration gradient, whereas regulation at the cell-blood boundary involves variations in concentration of organic substances, principally amino acids.

The excretory organs of the higher crustaceans, the antennal glands, function in essentially the same way as the metanephridia of annelids, the major structural modification being the reduction of the coelom to an end sac draining into a tubule which may be expanded and folded at its upper end to form a labyrinth and dilated at its lower end to form a bladder. The antennal glands, like the metanephridia, may function in ionic and in volume regulation. Many freshwater species such as crawfish and amphipods get rid of excess water and conserve ions by excreting a hypotonic urine (Lienemann 1938, Riegel and Kirschner 1960, Lockwood 1961). Marine, brackish water, and a few freshwater species produce a urine that is isosmotic with the blood but differs in ionic composition. For example, the magnesium level of the blood of most higher marine decapods is maintained at a lower level than that of the surrounding sea water by the activity of the antennal glands which excrete this ion. The urine has a higher magnesium level than the blood but a lower level of other ions so that the two fluids are isosmotic. Changes in salinity may produce changes in urine flow which may be accomplished by variations in the rate of movement of substances into the end sac or by variations in the rate of reabsorption of fluids, possibly under hormonal control, although this has not been proven.

In addition to being subjected to fluctuating osmotic conditions, it is characteristic of a number of estuarine species, including some commercially important crustaceans, to move across salinity gradients as a normal part of their life cycles. Environmental requirements differ at different life stages. The life cycles of the larger, motile crustaceans, principally shrimp and crabs, follow a general pattern characteristic of a number of estuarine species. Spawning takes place in high-salinity, offshore waters with the larvae then moving shoreward toward low-salinity, nutrient-rich estuarine waters to feed and grow. Sexual maturation is accompanied by migration back toward the sea where the cycle starts over again (Pearse and Gunter 1957).

Feeley and Wass (1971) gave a figure showing the salinity range of 21 species of gammarid amphipods found in lower Chesapeake estuaries. Three species were found in fresh water, seven at 10 ppt and sixteen at 20 ppt. The salinity range was 0 to 24 ppt.

A number of workers have noted that the white shrimp, *Penaeus fluvialis*, spawns at sea but the postlarvae enter low-salinity waters to develop (Viosca 1920,

Weymouth et al. 1933, Gunter 1950, Lindner and Anderson 1956). The blue crab, *Callinectes sapidus*, has a similar life cycle but differs in that mating takes place in low-salinity waters when the female is in the soft shell stage of the final molt. The adult female then moves seaward to spawn. Males need not be present in the spawning area and most of them remain in low-salinity, inshore waters. Several studies have shown that the larvae of *C. sapidus* will not develop normally in low salinity waters (Sandoz and Rogers 1944, Costlow and Bookhout 1959).

After reviewing some of the literature on brachyuran species Roberts (1971) stated, "Salinity strongly affects survival with tolerance ranges unique for each developmental stage and each species." He showed that eggs of the anomuran, *Pagurus longicarpus*, would not hatch at 10 ‰, hatched slowly at 15 ‰, and developed normally at 20–30 ‰.

Although the general patterns of osmoregulation of estuarine crustaceans are known, factors that might account for differences in salinity preference in the same or closely related species are not well understood. Adult male and female *C. sapidus* show some differences in osmotic response (Tan and Van Engel 1966, Ballard and Abbott 1969) but it is not certain that the differences are sufficient to account for observed differences in distribution. The near segregation of the sexes may be largely behavioral responses related to reproduction.

The three species of commercially important shrimp belonging to the genus *Penaeus* show differing salinity preferences. All three species have access to wide salinity ranges yet they distribute themselves by species according to salinity (Gunter, Christmas, and Killebrew 1964). In Texas waters the white shrimp *P. flaviatilis* is most abundant at salinities below 10 ‰, the brown shrimp *P. aztecus* at 10 to 20 ‰, and the pink shrimp *P. duorarum* at 18 ‰ and above. Commercial catch data correspond to field studies in indicating the salinity optima of the three species. Pink shrimp are taken in greatest abundance in the high-salinity waters of the Dry Tortugas of Florida and Campeche Bay of Mexico. The greatest numbers of white shrimp are taken in the Mississippi River estuarine area of Louisiana, where salinities are low, and the largest catches of brown shrimp are made off the dry, somewhat salty Texas coast. Differences in the lower salinity limits of the three species indicate that the observed differences in salinity preference may be related to differences in osmoregulatory ability but comparative studies of such responses have not been made. In the northern Gulf of Mexico *P. flaviatilis* has a lower limit of 0.42 ‰, *P. aztecus*, 0.8 ‰ (Gunter and Shell 1958), and *P. duorarum*, 2.7 ‰ (Hoese 1960). In keeping with the known fact that there is maximum invasion of fresh waters in tropical regions, *P. duorarum* occurs in lower salinities in southern Florida than is indicated above.

Whether the occurrence of *P. aztecus* and *P. duorarum* in lower salinities in the southernmost part of their ranges is related to increased osmoregulatory ability at high temperature is not certain. Temperature is known to affect blood concentration and salinity tolerance in a number of crustaceans but the effect is not the same for all species. In many there is an inverse relationship between temperature and blood concentration. This situation exists in such diverse species as the amphipod *Gammarus duebeni* (Kinne 1952, Lockwood 1967), the prawn *Palaemonetes varians* (Pannikkar 1940), and the crab *C. sapidus* (Rees 1966, Ballard and Abbott 1969).

When temperature drops blood concentration increases, and high temperatures result in lowered blood concentration. On the other hand, species such as the isopod *Asellus aquaticus* (Lockwood 1967) and the crab *Potamon niloticus* (Shaw 1959) show a drop in blood concentration with a drop in temperature, and increased blood concentration with increased temperature. Venkataramiah et al. (1974) noted the same thing for *Penaeus aztecus*.

There are also species differences in effect of temperature on salinity tolerance. *P. varians*, *Leander serratus*, *P. aztecus* and *P. duorarum* tolerate low salinities better at high temperatures. This phenomenon may account for maximum invasion of low salinities in tropical areas, as already indicated for *P. aztecus* and *P. duorarum*, or in the summer for some species such as *C. sapidus* (Hay 1904, Gunter 1938, Pearson 1948). Venkataramiah et al. (1974) found that *P. aztecus* tolerated wider salinity range at high temperatures. However, other species such as *Gammarus duebeni* and *Rhithropanopeus harrisii* tolerate subnormal salinities best at the lower part of their temperature ranges (Kinne 1964).

The juvenile brown shrimp, *Penaeus aztecus*, exhibited good ionic regulation of blood Na and Cl in a salinity range of 8.5 to 34.0 ppt at temperatures of 26 and 31°C, which they generally encounter in estuarine habitats (Venkataramiah et al. 1974). On the other hand, at low temperature, 21°C, the young shrimp seem to lose the ions to the media in low salinities of 8.5 and 17.0 ppt, while in the higher concentrations of 25.5 and 34.0 ppt there was a tendency towards a slight isotonicity with the external media.

In laboratory experiments juvenile brown shrimp exhibited 100% survival in a salinity concentration range of 8.4 to 34.9 ppt at an ambient temperature of 26°C (Venkataramiah et al. 1972, 1974). Sudden temperature fluctuations influenced the salinity tolerance of these shrimp, especially in abnormal concentrations outside the range of 8.5 to 34.0 ppt when tested over a broad salinity range of 0.34 to 59.9 ppt. At 26°C, the shrimp from the same temperature background exhibited better salinity tolerance in the entire salinity range than those tested at 21 and 31°C. Following a direct transfer from 26 to 31°C, the shrimp became hyperactive throughout the test media, more so in abnormal salinities, with the result that their chances of survival were impaired more than those tested at 21°C.

When the animals were preacclimated at 21 and 31°C and tested in the same media, it appeared that the low temperature (21°C) acclimated animals were adversely affected when they were forced to face sudden temperature rises as often happens in the estuarine conditions during summer. On the contrary, the high temperature (31°C) acclimated animals seem to face the sudden temperature fluctuations more successfully. However, the shrimp acclimated at medium temperature (26°C) conditions were far better equipped to meet the high or low fluctuations.

There are unexplained seasonal effects that appear to operate differently from temperature per se. The blood concentration of *Asellus* is higher in winter than in summer. Since there is a direct relationship between temperature and salinity in this species, it would be expected that low winter temperatures would result in lowered blood concentration (Lockwood 1960).

On the Gulf of Mexico and the South Atlantic coasts of the United States, most of the important fishery organisms are tied to the estuaries because of their life histories. Most of them spawn in high-salinity waters and move back into the bays in larval or very young stages. There they begin to grow and then move toward the sea. This puts them in ever increasing salinities as they become larger. Some of them may return to the estuaries after spawning and this is especially true of fishes which have a life cycle of a few years. On the other hand, the short-lived species, such as the shrimp especially, never return to low-salinity waters. Thus many species of fishes show larger fish in saltier waters and smaller fish in low-salinity waters and in the shrimp there is a close relationship between size and the salinity gradient. These matters have been set forth in Gunter (1945, 1947, 1950, 1956a, 1961a,b,c, 1967a) Gunter, Christmas and Killebrew (1964) and Pearse and Gunter (1957).

There is some indication from the field data that younger shrimp can withstand lower salinity than the larger shrimp. In any case, only smaller shrimp are found in the low-salinity, cool waters of the estuaries during the winter. Physiological proof of this observation was shown by Venkataramiah et al. (1974) who, by salinity tolerance studies made with the different size groups of brown shrimp, *Penaeus aztecus*, postlarvae of 13–20 mm and two sizes of juveniles of 21–45 mm and 50–75 mm, showed that salinity tolerance was related to size. Among the three groups, the postlarvae exhibited 100% survival in 8.5 to 51.0 ppt salinity while the juveniles in the increasing order of their size exhibited mortality in 51.0 ppt and 47.6 ppt salinities respectively. However, in salinities below 8.5 ppt, although the postlarvae survived better numerically, the juveniles survived longer in the same stress media before their death.

The blue crab, *C. sapidus*, became very scarce in south Texas bays during a drought that culminated in the dry year of 1966, and was replaced by *C. danae*, a high-salinity species generally found offshore. After the drought was broken, *C. danae* disappeared from the bays and was replaced by *C. sapidus* (personal communication S. H. Hopkins). It has been shown that commercial production of the white shrimp, *P. setiferus*, a low-salinity shrimp, is directly correlated with rainfall of the Texas coast, apparently because salinity is a limiting factor to this shrimp on this rather dry coast. On the other hand, the high-salinity shrimp, *P. aztecus*, shows no correlation with rainfall on the same coast (see Gunter and Edwards 1969). In Louisiana waters Barrett and Gillespie (1973) found a rather close correspondence between river discharge and brown shrimp production in the Barataria-Caminada area; they also found that salinity and annual production were related and that the optimum for brown shrimp seems to be around 19 ppt.

The commercial shrimp of the family Penaeidae, composed chiefly of three species along the South Atlantic and Gulf coasts have for a number of years supported the most important fisheries in North America. Consonant with their commercial and biological importance, they have been rather extensively studied. Certain people, chiefly laboratory scientists, or those who have devoted time to the open ocean rather than to the estuaries, have questioned some of the ideas set forth above. In part the questions are erroneous, or they are based upon a misunderstanding. As a side issue almost, in the beginning we might say that much has been made of the statement by Lindner and Anderson (1956) that the size gradient of shrimp

is correlated more with locale than with salinity. As a matter of fact, Lindner and Anderson only made this statement and did not prove it. Furthermore, it will be logically a very difficult matter to handle because year in and year out points in the bays, sounds and passes, the locales have an average and characteristic salinity.

Actually, the three common penaeid shrimp, the white shrimp, *P. fluvialis*, the brown shrimp, *P. aztecus*, and the pink shrimp, *P. duorarum*, are almost completely euryhaline, in that they are found in almost fresh water and in pure sea water and even in hypersaline water, at various stages of their life history. Apparently the shrimp are osmoconformers and can acclimate to a great range of salinity, as would be expected of an organism that lives over a wide salinity range. Nevertheless, the statements of Zein-Eldin (1963), Zein-Eldin and Aldrich (1965) and Parker (1970) that salinity has little effect on distribution, survival, growth and, by implication, on other biological phenomena of shrimp are simply untenable and in some ways can be disproven by their own papers. In fact this can only be true when we find shrimp spawning, eggs hatching, larvae living and juveniles growing up in the same salinities and the same place.

In her 1963 paper, Zein-Eldin showed that shrimp at salinity levels of 2-5-10-25 and 40 ppt grew about as well at all of these salinities except at 40 ppt where the final results of growth were about 70% less. Growth at 2% and 5% was actually higher than at the other salinities. The initial material was postlarval shrimp seined from nearby surf zones, which means the Gulf beach. The shrimp were approximately 5 mg in weight, but the lengths are nowhere clearly set forth. Furthermore, the species were mixed as the author states, and the mortality rate is not given. The author states that growth rate between 2 and 40 ppt is not significantly different. The data in this paper are impossible to analyze as presented, but they leave the impression that shrimp will grow over a wide salinity range.

The paper by Zein-Eldin and Aldrich (1965) gave results of two sets of studies at salinities ranging from 3 to 41 ppt. The animals were caught in the surf and kept for 24 hours at a salinity of 24-25 ppt and temperature of 24-26°C. They were then placed in the varying salinities at temperatures of 7-15-25-30 and 35°C. In all 600 shrimp were used. The results are summarized as follows:

Salinity (ppt)	3-7	8-11	23-27	32-34	36-41
Mortality (Percent)	49.0	35.5	10.8	7.5	18.5

The results show the highest mortalities were at the lowest salinities and the lowest mortality was at the range 32-34 ppt after a 24-hour period. This is all to be expected, for 12-mm postlarvae were subjected to the greatest abrupt osmotic change at 3 ppt, and so on. This proves what was generally known before, namely the greater the abrupt salinity change the higher the mortality, whether it be up or down.

In the second experiment 100 animals each were placed in the salinities shown below at temperatures of 11-18-25 and 32°C. The shrimp were kept 28 days.

Salinity (ppt)	2	5	15	26	35	Average
Survival (Percent)	5.2	51.8	80.8	87.8	94.0	63.9

There was almost a 95% mortality at a salinity of 2 ppt and the greatest survival was at a salinity of 35 ppt. The results actually show that the small shrimp live better at high salinities. This is of no particular comfort to proponents of the idea that shrimp do better in low salinities or to proponents of the idea that salinity does not make any difference. Additionally, the total mortality was 37% in 28 days and except at the two highest salinities, nearest to that from which they came, the experimental shrimp were not living under a situation which would have carried them through the summer.

Recent work at this laboratory has shown that postlarvae survive high salinities better than juvenile shrimp, as would be expected from the life history.

We have found that wild populations of shrimp are true to their name, being wild, and agonistic or even antagonistic and that they introduce disease into the laboratory.

In accordance with what may be called Lund's Dictum, because he continually emphasized it (E. J. Lund, personal communication), we feel that experimental animals should be those of known history, living and growing under conditions that are known, normal and controllable. Under these conditions with a mortality rate of about 2% of the 640 experimental animals in six weeks time, it was shown by Venkataramiah, Lakshmi and Gunter (1974) that brown shrimp grow fastest and utilize their food most efficiently at 8.5 ppt and 15 ppt salinity as compared with all higher salinities. These observations correspond with field observations that small shrimp are found mostly in low-salinity waters, which presumably they seek out.

Parker (1970) says, "no evidence is presently available to indicate that immature brown shrimp cannot thrive and grow in salinities ranging between 1 and 35 ‰." This remark is refuted by the paper of Zein-Eldin and Aldrich (1965) which showed poor survival at 5 ‰ and below. Parker also implies that data from one bay (Galveston) are better than data from the whole Texas coast for showing brown shrimp distribution. He does not mention that the University Marine Science Institute was carrying on a large project which assumed a detectable, low level of harmful pollution in all Galveston Bay waters, nor that the proportion of high salinity waters westward and southward on the Texas coast make Galveston Bay and the whole coast difficult to compare. The data of Gunter, Christmas and Killebrew (1964) remain the best and most extensive for the distribution of brown shrimp in Texas as a whole.

Parker's data show, if anything, that he found the small shrimp were most abundant at lower salinities, which Gunter has contended for a long time. Gunter's idea, more or less inherited from Percy Viosca, applied chiefly to the white shrimp, *Penaeus flaviatilis*, but that shrimp is declining everywhere now and the brown shrimp is taking over its ecological niche, and is being found at low salinities where apparently it was not seen abundantly in former years.

Q. PHORONIDA. This is a phylum of benthic worms living in tubes in the bottom from low water down to about 30 fathoms. Some live with or in the shells of other animals. They are protostomes and have a larva called an actinotroch which is a sort of aberrant trochophore. The most distinguishing character is a horseshoe-shaped circle of cilia-covered tentacles at one end, called the lophophore. The digestive tract is looped and both ends lie within the lophophore. This latter organ relates the group to the Bryozoa and the Brachiopoda.

Some phoronids are estuarine and Wass (1963) reported the Chesapeake Bay species, *Phoronis architecta* at salinities as low as 18.0. Larvae have been seen in the Gulf of Mexico, but adults have not been reported (Hedgpeth 1954b). This is another rather unimportant group from the ecological point of view.

R. BRYOZOA or ECTOPROCTA. This phylum is made of colonial animals growing in arborescent colonies or flattened encrusting mats as "fouling" organisms. The individuals are quite small but some of the arborescent colonies are somewhat impressive. Each individual has a lophophore which can be withdrawn with the mouth. The anus opens just outside the lophophore. Encrusting forms live individually in what is essentially a small calcareous box. Some species have avicularia, somewhat like the pedicellariae of the echinoderms, which act as antifouling mechanisms. The bryozoa are nearly all marine, but there are a few fresh water species. Their mass is comparatively small and except as fouling organisms they are not of much ecological significance.

In one species, *Zoobotryon pellucidum*, in the shallow Gulf of Mexico the zooids are on long chitinous stolons and the colonial masses wash up in windrows on the outside beaches and are sometimes abundant enough to interfere with fishermen's trawls (Gunter 1950). He reported none at salinities below 35.0. Christmas and Langley (1973) reported *Bugula neritina* in Mississippi Sound at 2 to 35.5 ppt saline, with over half the specimens taken at 25 to 30 ppt, but they added that many were probably dead when taken. It seems safe to conclude that this common species lives mostly above salinities of 25 ppt. Gosner (1971) listed 20 Atlantic species as euryhaline among a total of 120 recorded, but the term is probably quite loosely applied. The most widespread bryozoan, *Victorella pavida*, reported from England, Egypt, Japan, Australia, India and Chesapeake Bay, is said to tolerate salinities from fresh water to 27 ppt (Brattstrom 1954).

S. BRACHIOPODA. The brachiopods are coelomate, lophophorate protostomes, all benthic and all marine. They have a pedicel passing out between the unequal shell valves. They feed on plankton and detritus. They are not estuarine and apparently not often subject to low-salinity waters. *Crania* and *Lingula* have existed without much change since the Ordovician (see Berry 1929). They are not abundant today, and mostly confined to offshore waters and are not often seen. Their ecological importance is small.

T. CHAETOGNATHA. This is a dart-shaped group of organisms with fins, and a circle of chitinous spines around the mouth. Arrow-worms have no circulatory or excretory systems, but they have a large "brain" and nervous system. One genus is benthic but all the others are drifting free as nekton. They are generally motion-

less but are capable of sudden swimming movement after prey. They are quite small, the largest species being only a few inches long, but they are present in enormous numbers at times and they are voracious feeders on copepods, larvae of all kinds and any animal they can subdue. Thus they are important components of the plankton.

Pierce (1954) has listed 14 species from the Gulf, 5 from inshore waters. Salinity relations are not mentioned. Gosner (1971) says a few species enter estuaries but that they are more common in "relatively undiluted" sea water. Cronin et al. (1962) recorded *Sagitta elegans* in water as low as 11.4 ppt in Delaware Bay.

U. POGONOPHORA. This peculiar group of animals lives in tubes in the abyss. Strangely, there is no alimentary tract and all digestion is done outside the body and within the tubes. The animals are very elongate. Anatomical and developmental characters show affinities to the Hemichorda. Recently several new species have been described from the South Atlantic and Gulf. They will be among the last animals on Earth to feel the effects of anything man does to the sea.

V. ECHINODERMATA. The echinoderms are coelomate, radial animals with five branches. They are generally covered with calcareous platelets and spines except for the sea cucumbers which are soft-bodied. The coelom branches into small tubular extensions which extend through the body wall and perform several functions. In the starfish they are organs of locomotion. The early echinoderms of the Cambrian are all bilateral and not radiate. Modern species are all marine. They have the modified diploblastic larva that shows kinship to the lower chordates. They feed on detritus, plankton and various molluscs, and they are quite adept at catching certain motile animals. In general they are high-salinity organisms and are not often taken in estuarine situations.

Hedgpeth (1950) recorded five species of starfish, sea urchins and sand dollars from the Texas coast jetties of the passes to the Gulf. Gunter (1950) took three species in trawls. The lower salinity range for each species (*Mellita quinquesperforata*, *Astropecten articulatus* and *A. duplicatus*) was 29.7 ppt. Five specimens of *A. articulatus* were taken in an inside channel near the Gulf. All the others were in the open sea.

In Pine Island Sound, Florida, Gunter and Hall (1965) took 378 specimens of sand dollars, sea urchins starfish, and serpent stars and one sea cucumber, comprising 11 species and 3,000 specimens of the serpent star *Ophiolepis elegans*, at salinities ranging from 21.4 to 37.2 ppt. The average low-salinity range for all species was 23.5.

Gosner (1971) notes that Atlantic coast starfish in general show little tolerance for low salinities, but says that *Asterias forbesi* and *A. vulgaris*, well-known oyster enemies, can survive in waters of 14 and 18 ppt respectively. He also lists *Urasterias lineki* as being found in salinities as low as 15 ppt.

In general the echinoderms live in high-salinity waters and are not subject to the saline changes of the bays. Starfish predators of oysters do not exist in the Gulf of Mexico.

SOME GENERAL CONCLUSIONS AND COMPARISONS CONCERNING INVERTEBRATES

Except for certain flagellates and ciliates that are numerous in the plankton the protozoa are not greatly important to the life of most estuaries. In many areas at certain salinities, lack of sufficient circulation and the accumulation of organic materials and nutrient salts lead to flagellate plankton blooms. This in turn leads to fish-kills through the production of poison or by consumption of dissolved oxygen.

Certain ctenophores are quite abundant in estuarine waters where they are very important consumers of larval fishes, bivalves, crustaceans and other ctenophores (c.f. Gillespie 1971). When the salinity of their environment is changed beyond their internal tolerance range they are killed in great numbers.

The various worms and related sessile or burrowing organisms can withstand sudden freshets or floods by pulling back into their holes or closing up. Many polychaete worms are highly motile and can escape salinity changes by swimming. The mass of these animals is considerable and they are important ecologically as food animals. Certain species will be killed by severe salinity changes, but even so, growth and reproduction are fast and life cycles are generally short. When salinity reverts to normal even after a considerable kill the worms return quickly. In cases of permanent salinity changes various species are moved up and down the bay.

Crustaceans are best represented in estuaries by the higher decapods such as shrimp and crabs which, in addition to being efficient osmoregulators, are motile. Adults are not likely to be killed by salinity changes, but may move to more preferred salinities. It is now recognized that cool springs with flood waters kill incoming brown shrimp larvae, which causes a bad shrimp year.

The estuarine molluscs are sessile or feebly motile. They can withstand excessive fresh or salty water for a time by closing up but extended osmotic extremes will kill them, either directly by producing changes in blood concentration beyond their tolerance range or indirectly by favoring predators and disease organisms.

Since species drop out along the decreasing salinity gradient in estuaries, fewer species are present than in the marine environment. However, there are often larger numbers of individuals of each species, possibly due to decreased competition. The individuals tend to be small, sometimes because the low salinity is close to the limit of tolerance, but more often because estuaries are nursery grounds for younger animals which must reach such areas to develop (Gunter 1961a, 1967b). The same pattern of decrease in number of species, increase in number of individuals, and decrease in size occurs in hypersaline waters, but such areas are not required for completion of life cycles.

Salinity limits are sometimes quite sharp. Segerstråle (1953) reported extension of the range of a number of marine species when salinity in certain areas of the Gulf of Finland rose from 5.2 ‰ to only 5.8 ‰. Dahl (1956) comments that in the Skagerrak, 75% of marine species disappear with a drop in salinity from 34 ‰ to 30 ‰. A number of workers have shown that the distribution of invertebrates in estuaries and hypersaline lagoons show definite patterns related to salinity (Ladd 1951, Gunter 1956b, Parker 1959). Correlations between seasonal salinity changes

and distribution have been demonstrated (Gunter 1950, Gunter et al. 1964), as well as effects of long periods of drought (Gunter and Hildebrand 1954, Hoese 1960) and floods (Gunter 1952).

Whether the limits are physiological, ecological, or behavioral, and whether they are imposed on early stages of the life cycle or on adults, salinity has an effect on distributions of animals. Large changes will clearly affect distribution patterns as some forms are killed and others move, either immediately or in successive steps in successive generations. Even regulators vary in degree of regulation, with each species having its own salinity limits and salinity preference, so that any large or long-term change in salinity will result in changes in the composition of the fauna of the area affected.

Low-salinity periods, freshets and floods may be the norm in most estuaries and in killing out predators, parasites and competitors they seem to benefit oyster beds from time to time, and possibly crustaceans, too, as during the Bonnet Carré Spillway openings.

W. HEMICHORDATA. The chordate animals are basically characterized by a dorsal supporting rod, the notochord, above the intestine, a tubular nervous system lying above the notochord and gill slits in the pharynx. In the true Chordata all of these characters are clear and sharp. A wormlike group, of two quite different types and showing some of these features, have been thrown together as the Hemichordata.

These two groups are the Pterobranchia and the Enteropneusta. The first has few or no gill slits but they are abundant in the latter. The Pterobranchia have a solid nerve chord, while the Enteropneusta have a dorsal nerve tract which is tubular anteriorly. Both groups have a diverticulum of the foregut, which is said to be a primitive notochord because of the similarity of embryonic origin with the notochord of amphioxus. On the other hand, the embryogenesis and the dipleurula larva show affinities of the two groups and relations to the Echinodermata.

The Pterobranchia are nearly all from deep water. A few species are found intertidally in the tropics. They have plumes extending from near the gill slits used in food capture. They are not common.

The Enteropneusta, commonly called acornworms, are found in the shallows of all seas of the world. They are wormlike with a proboscis, and a collar under which the mouth opens. They have numerous gill slits. Osmoregulation characteristics are unknown but these animals live in the bays in Mississippi and Texas where they are sometimes subjected to quite low salinities.

Acornworms live in u-shaped tubes in the mud and they are extremely soft. There is an unnamed giant species in Louisiana and Mississippi bays near the river. It may be three feet in length and breaks under its own weight when picked up. *Saccoglossus kowalevskii* is found on the Gulf and Atlantic coasts. Gosner (1971) lists it as euryhaline.

The acornworms smell strongly of iodoform and sometimes chloroform. At times the commercial shrimp and bottom feeding fishes of the shallow Gulf of

Mexico waters take on the same odor reputedly from feeding on acornworms. If the surmise is correct, the acornworms must be much more numerous than is generally realized. Salinity relations are unknown.

X. PROTOCHORDATA. All members have the dorsal, tubular nervous system, gill slits and well-developed notochord at some stage. The group could be included under the Chordata which would then be separated into the Acraniata and the Craniata. The Acraniata are the tunicates or sea squirts and Amphioxus. The sea squirts begin with a tadpole-like larva with a well-defined notochord. This is lost when the animal sets individually on the bottom or forms colonies by budding and sometimes floats on the high seas. A small individual species, *Molgula manhattensis*, is found in the lower bays of the Gulf of Mexico and South Atlantic coast. Gunter and Hall (1965) reported it at 27.5 ppt salinity in the Caloosahatchee Estuary, Florida. The salinity ranges of three other species were: *Molgula occidentalis* at 22.5-34.2 in the Caloosahatchee Estuary and San Carlos Bay; *Styela plicata*, 24.8-33.8 San Carlos Bay, *Amaroucium stellatum*, 24.5-35.0 San Carlos Bay.

Gosner (1971) lists *M. manhattensis* as euryhaline because it is found where the water drops to 10 ‰ in the Patapsco River. But the animals die off in the winter and this little solitary tunicate is far from being euryhaline.

The Cephalochorda or Amphioxus have as fine a notochord as any animal but their head amounts to nothing and even the nerve cord does not end in a frontal ganglion, and the only skeletal element is the somewhat stiff notochord itself. The lack of a cranium sets the amphioxo off from all higher chordate animals. They have a circle of tentacles around the vestibule in front of the mouth and running from the mouth down the pharynx is a peculiar ciliated canal, the endostyle, which helps move the food and possibly to digest it. Supposedly it is the progenitor of the thyroid gland of higher organisms. An endostyle also exists in the pterobranchs, the balanoglossids and the tunicates, further establishing the kinship of this strange assortment of animals.

The lancelet-like amphioxus lives in the bottom and will dive in quickly and out of sight either head first or tail first. In Mississippi Sound it was never found on fine sand or clay, but on mixtures of coarse sand and silt. Boschung and Gunter (1962) reported a maximum of 72 animals per square meter over an area of several square miles, involving a population in the billions. The mean salinity was 24.3 and the range was 15.4 to 33.1 per mille. The species was *Branchiostoma floridae* Hubbs.

Later on Dawson (1965) showed that the lancelet population in Mississippi Sound was practically annihilated by low salinities following heavy rains and flooding on the Mississippi coast. So it is apparent that low salinities will kill amphioxus on the Gulf coast and that they are organisms of some trophic importance.

Y. VERTEBRATA. Among the vertebrates the groups that are affected directly and greatly by salinity change are essentially those with a living skin and which breathe through the water. They are truly aquatic. They are the Cyclostomata (hagfishes and lampreys), Elasmobranchii (sharks and rays), Osteichthyes (true fishes) and Amphibia (frogs, salamanders, etc.). Of these only the hagfishes are completely marine and only the amphibia are primarily fresh-water.

Almost all fishes have internal salt concentrations different from that of their external environment and so must solve osmotic problems. Among the amphibians, a very few species of frogs and toads occur in brackish waters. Marine reptiles and mammals do not have the same problems as fishes in that they do not have permeable respiratory surfaces exposed to the environmental water. Nonetheless, they lose water in excretion of nitrogenous wastes and by respiratory evaporation, and this loss must be made good in some fashion. Certain birds that spend considerable time at sea or feed on sea life are classed as marine.

Of vertebrates occurring in coastal areas, particularly in estuaries, some are more or less permanent members of the fauna but many are temporary inhabitants consisting of many essentially marine forms able to withstand low salinities, a few invaders from fresh water, and species that migrate back and forth between the sea and fresh water. Of particular importance are those species which must spend parts of their life cycles in estuarine waters.

Many of the general considerations already described for invertebrates also apply to vertebrates. They, too, vary in their ability to tolerate salinity changes. Most species can osmoregulate and thus hold changes in internal osmoconcentration to a minimum. Some can only hyporegulate; others can only hyperregulate. Such species are, of course, stenohaline. A large number of vertebrates are, however, euryhaline and withstand more or less wide variations in salinity. They do so by tolerating changes in internal osmoconcentration, by varying the rate of osmoregulatory activity, or by both hyporegulating and hyperregulating.

The same major organs are involved in osmoregulation in vertebrates as are used by invertebrates; namely, the gut, gills and excretory organs. The skin of amphibians presents a permeable surface across which water and salts may pass, but the integument of other quadrupeds is virtually impermeable to these substances. Certain vertebrate groups have additional structures for excretion of excess salts. Examples are the rectal glands of sharks and the nasal and orbital glands of marine birds and reptiles.

Some scientists accept the theory that vertebrates have secondarily invaded the sea from a fresh water, or fresh water to land to sea origin and that, since adaptation can only involve modification of structures already present, marine species have had to make use of kidneys originally adapted for handling osmotic problems imposed by a freshwater environment. Most biologists question a freshwater origin of all vertebrates although the typical fish kidney may have developed in dilute sea water or in fresh water (Pearse and Gunter 1957). But the kidney of the highly marine hagfishes seems to be primitive or structurally similar to that of freshwater fishes, and this group has no known freshwater ancestry. In any case, the kidney of all vertebrates is based on the same general plan typified by the "primitive" kidney of freshwater fishes. Therefore, a brief review of its structure is in order. A detailed review has been presented by Hickman and Trump (1969).

The kidney of freshwater fishes is adapted to excretion of excess water taken into the body by osmotic inflow to a more concentrated internal environment and to conservation of salts that tend to diffuse outward to a more dilute external environment. The organ is made up of varying numbers of basic units, the nephrons.

Each nephron consists of a knot of capillaries, the glomerulus, surrounded by a space, the Bowman's capsule, which is drained by a long, variously looped tubule. The tubule is, in turn, surrounded by capillaries; and certain parts, such as the proximal and distal convoluted tubules plus various intermediate segments, are specialized for specific functions. Blood enters the glomerulus under pressure; and various materials, including salts and water, are filtered through the capillary walls and the Bowman's capsule into the tubule. As the ultrafiltrate passes down the tubule, certain substances are reabsorbed by way of the peritubular capillaries, and some secretory products are added to form the final product, the urine. The kidney has a number of functions, but the handling of water, salts, and sometimes certain organic products such as urea is of importance in osmoregulation.

Obviously, if there is maximum passage of water from the blood into the tubules, minimum water reabsorption, and maximum salt reabsorption, a relatively large volume of dilute urine will be formed. Such is the case in freshwater fishes. On the other hand, if there is little passage of water into the tubules, maximum water reabsorption, and little salt reabsorption, the urine will tend to be scanty and concentrated. This is the general pattern of kidney function in marine fishes. It should be noted that a large glomerular surface favors water passage into the blood, and a well-developed distal convoluted tubule is associated with salt reabsorption. In addition, in some vertebrates, chiefly the sharks and their relatives, but also in the coelocanths and certain frogs, urea and trimethylamine oxide reabsorption is of importance in osmoregulation.

The kidney is not the only organ involved in maintenance of a proper water-salt balance. Salts passively diffuse across the permeable gill membranes and are lost from freshwater fishes and taken up by marine fishes. However, the gills are able to compensate for these movements by active uptake or secretion of salts against a concentration gradient. Thus they serve as important extrarenal pathways for salt exchanges. The rectal, nasal, and orbital glands of certain marine groups have already been mentioned as functioning in secretion of excess salts.

Adaptation to the variety of habitats in which vertebrates occur involves the use of one or more of the osmoregulatory mechanisms described above.

REMARKS ON GENERAL CLASSIFICATION

It was stated above that we would follow the general phyla of the Animal Kingdom and we have done so without particularly noting the larger groupings.

Animal life begins with populations of unicellular organisms feeding as animals. The early Protozoa were probably derived from algae as shown by the similarity of the Flagellata to the algal germ cells.

These changed by simple association into the Parazoa and Metazoa. The Parazoa or sponges are a sideline group and the Mesozoa are of uncertain affinity. Presumably the Metazoa or Eumetazoa are more closely akin.

The so-called Radiata or radially symmetrical forms, the Coelenterata and the Ctenophora, are two-layered organisms with an endoderm and ectoderm. They may

be called the Diploblastica. Affinities with the next higher group, the flatworms, are a matter of argument but some crawling ctenophores resemble flatworms.

All remaining organisms are triploblastic and bilateral. The most primitive group with a solid mesoderm with no spaces is comprised of the Platyhelminthes and Nemertea. These two phyla are the only bilateral Metazoa without a body cavity between the alimentary tract and the body wall. They are known, therefore, as the Acoelomata.

The next group has a body cavity or a series of them but there is no epithelial lining and they are not of mesodermal origin and arise from the blastocoel, so they are said to be pseudocoeloms and the animals collectively are called pseudocoels. These phyla are the Aschelminthes, Acanthocephala and the Entoprocta.

The remaining phyla of the Kingdom Animalia all have a coelom, although in some it is very small. They are further divided by the Protostomia and the Deuterostomia distinction. The protostomes have spiral, determinate, total and unequal cleavage, with the mouth developing at the blastopore or original opening of the gastrula. This is the flatworm, annelid, molluscan, crustacean line. The larva is always a trochophore or modified trochophore, except in the Crustacea. It includes several miscellaneous worm groups and a group of animals with a lophophore, a coiled, tentaculate, ciliated feeding organ in the Phoronida, Ectoprocta and Brachiopoda. The lophophorate animals have some deuterostome characteristics and are placed last in the Protostomia series, which begins with the acoelomate flatworms and nemerteans and may be more fundamental than the presence or absence of a coelom.

In the Deuterostomia the cleavage is radial, generally holoblastic and indeterminate, that is a separate animal will develop from each blastomere. The blastopore of the gastrula becomes the anus. Essentially this is the chordate related line. The recognized phyla are the Chaetognatha, Pogonophora, Echinodermata, Hemichordata, Urochorda, Cephalochorda and Vertebrata. The last four are the superphylum Chordata. The echinoderms show their connections with the Hemichordata by the similar dipleurula larva and a dorsal nervous system. The hemichords show their relations to the higher chordates by the dorsal, tubular, ectodermal nerve cord and a small, anterior gut infundibulum which embryologically seems to be a notochord. The Urochorda and Cephalochorda have an excellent notochord, at least for part of their life, but they are separated from the higher Chordata because essentially they are headless and could be called the Acraniata.

As yet we do not know enough to discuss osmoregulation and salinity relationships along phyletic or evolutionary lines, but it is a matter to be held in mind by future workers.

OSMOREGULATION IN FISHES IN GENERAL

Because a great deal of the coastline of the United States is bordered by estuaries, and because estuaries are areas of variable salinity, fishes of coastal waters are largely euryhaline species. Not only must they tolerate typical salinity variations

of the estuary but, in addition, many species are migratory and cross salinity gradients in their migrations to and from the estuary or through the estuary. Anadromous and catadromous species represent extreme euryhalinity in their lifetimes for a part of their life cycle is spent in an oceanic environment and a part in fresh water. Yet, at any given stage they may be stenohaline (Krogh 1939, Huntsman and Hoar 1939, Black 1951b). Other euryhaline species may move freely across salinity gradients. Like estuarine invertebrates, a great many coastal fishes grow up in low-salinity waters, especially at smaller stages, and they seem to have a proclivity at this time for invading low-salinity or even fresh water (Gunter 1957b), whereas the adults are seldom or never found there. Günther (1880) pointed out this relationship for the common herring in the Thames Estuary many years ago.

Although the emphasis of the present discussion is on coastal species, nearly all euryhaline fishes osmoregulate in the same manner as freshwater fishes when in fresh water and in the same manner as marine fishes when in sea water. Thus a discussion of osmoregulation of coastal fishes must include some remarks concerning the special problems imposed by freshwater and marine habitats, as well as those that must be solved in adapting to varying salinities.

Smith (1932) is generally credited with giving the first comprehensive description of osmoregulation in fishes, but several earlier papers by Sumner (1905, 1906, 1907 and 1912) indicate that the basic mechanisms were known much earlier. Among scientists who have given reviews on osmotic processes in fishes are Black (1957), Gordon (1964), Parry (1966), Holmes and Donaldson (1969), Hickman and Trump (1969), and Conte (1969).

OSMOREGULATION IN FRESHWATER FISHES

Aspects of water and salt regulation in freshwater fishes have already been mentioned in describing general kidney function. As with all freshwater animals, fishes have a body fluid osmoconcentration greater than that of the surrounding water. In order to maintain this situation they must compensate for osmotic inflow of water and loss of salts by diffusion. The kidney is well adapted for this purpose. The relatively large glomerular surface allows for passage of considerable water into the kidney tubules. The tubules have low water permeability, but they strongly absorb monovalent ions. More than half of the filtered water is excreted, yet only small amounts of sodium and chloride are lost in the dilute urine.

Although the glomerular kidney possessed by nearly all freshwater fishes presents a large filtration area which facilitates water excretion, it is not necessary for survival in fresh water. Several species of pipefish occur in fresh water (Grafflin 1937, Whatley 1962). Like the marine members of their family (Syngnathidae) they possess aglomerular kidneys (Grafflin 1937). Occurrence of this type kidney in freshwater fishes is rare and possibly indicates recent immigration from the sea (Potts and Parry 1964a). The typical kidney of freshwater fishes is of the glomerular type, and biologists have demonstrated a relationship between degree of glomerular development and salinity of habitat (Marshall and Smith 1930, Lozovik 1963). Ogawa (1961) described atrophy of the glomeruli of freshwater goldfish adapted to one-third sea water.

Kidney reabsorption conserves salts but does not replace all those lost in diffusion and excretion. An additional extrarenal uptake of salts occurs. Sumner (1905) found that the general integument of bony fishes is impermeable to salts and suggested that the gills are sites of salt transport. Keys (1931) and Krogh (1937, 1939) demonstrated that such is the case. Keys and Willmer (1932) designated specific cells of the gill epithelium which they believed to function in osmoregulation as "chloride secreting cells." Although there is not universal agreement as to their role in osmoregulation, there is evidence that these same cells may function in salt absorption and in salt secretion (Pettengill and Copeland 1948, Copeland 1950, Philpott and Copeland 1963). The function of the cells is postulated to be transport of chloride, and probably other monovalent ions, against a concentration gradient from an area of lesser concentration to one of greater concentration. Thus, these same cell types could be utilized by freshwater, marine, and euryhaline fishes, with the direction of salt transport depending on the relative internal and external concentrations (Black 1951a).

Certain species of otherwise anadromous groups of fishes are confined to fresh water. Examples are the several water lampreys which are stenohaline. There are also certain freshwater trouts which are confined to fresh water, belonging to the genus *Salmo*. But when the trout are experimentally placed in sea water they show the same tolerance as anadromous races of the same species (Gordon 1959, Conte and Wagner 1965), such as *Salmo gairdnerii*, which is the rainbow in fresh water and the steelhead when it goes to sea.

A number of elasmobranchs occur in fresh water. Most are euryhaline but some are true freshwater species. Elasmobranchs handle their osmotic problems in a different manner than teleost fishes, and the special problems of the freshwater species will be taken up with the general discussion of this primarily marine group.

OSMOREGULATION IN MARINE FISHES

A. TELEOSTS. Most marine fishes are hyporegulators. Primitive hagfishes and elasmobranchs are exceptions and will be considered separately. The osmoconcentration of the body fluids of marine teleost fishes is less than that of sea water, hence these fishes face an opposite condition to that faced by freshwater fishes. There is a constant osmotic loss of water which can only be replaced by drinking of sea water. Excess salts, taken in with the ingested water together with those that diffuse inward, must be excreted from the body. There are three different ion excretion pathways, with the gills being the most important in osmoregulation. Water, monovalent ions, and some divalent ions are absorbed from the gut. Most of the magnesium and sulfate ions are not absorbed and pass through the gut to be excreted with the feces. The small amounts of these ions that are absorbed are secreted into the kidney tubules and eliminated with the urine. Excess monovalent ions are transported across the gills to the outside, presumably by the chloride secreting cells.

The kidneys of marine fishes are based on the typical vertebrate plan but show varying degrees of degeneration of certain parts. Since osmotic flow of water is outward rather than inward, little is filtered into the kidney tubules. Therefore,

a large glomerular surface is not advantageous to marine fishes. The kidneys of some species, such as pipefishes, sea horses, toadfish, midshipmen, and angler fishes are totally or partially aglomerular (Edwards 1928, Marshall 1929, Marshall and Smith 1930, Ogawa 1962). In some species the neck section between the glomerulus and tubule is restricted, and in others the vascular supply is reduced to the extent that the glomeruli are nonfunctional (Potts and Parry 1964a, Hickman and Trump 1969). These features might be considered modifications for a marine existence. However, many marine fishes have functional glomerular kidneys and, as previously noted, certain freshwater ones do not. In any case, reduction of the glomeruli is not disadvantageous to marine fishes and it has occurred in several groups. In addition, the distal convoluted tubule is often absent (Hickman and Trump 1969). Its salt reabsorptive function is of little value to marine fishes since their need is to excrete salts.

In summary, marine teleosts maintain a normal body fluid concentration by drinking sea water, excreting excess salts largely by way of the gills, and eliminating a small amount of urine that is nearly isosmotic with the blood. The kidneys seem to function primarily in elimination of magnesium and sulfate ions.

B. HAGFISHES. Blood of primitive hagfishes is essentially isosmotic with sea water. The two fluids have nearly the same sodium and chloride content although they differ in ratios of other ions such as magnesium, sulfate, potassium, and calcium (Robertson 1954, 1963, McFarland and Munz 1965, Morris 1965). There is virtually no net exchange of salts and water between the body fluids and the surrounding sea water.

The kidney is glomerular but the filtration rate is low, and neither sodium chloride nor water is reabsorbed from the tubules (Munz and McFarland 1964). The kidney is not needed for osmoregulation and it serves primarily for ionic regulation.

Possession of blood isosmotic to sea water and no mechanism for salt reabsorption points to a marine origin of hagfishes. Yet they have glomerular kidneys which lend themselves to excretion of excess water. Hickman and Trump (1969) suggest that possession of such kidneys may be of survival value since hagfishes sometimes occur in waters of varying salinity, but this theory is doubtful. The idea is unlikely. These fishes are highly permeable to water (McFarland and Munz 1965), and survival in dilutions of sea water would presumably require a mechanism for excreting osmotically derived water at approximately the same rate that it enters. The large filtration area provided by the glomerular kidney would facilitate passage of water into the tubules and, since water cannot be reabsorbed, would contribute to formation of increased amounts of dilute urine. Studies by McFarland and Munz (1965) on the hagfish, *Polistotrema stoutii*, showed an initial rapid gain in weight when exposed to 80% sea water but the weight returned to normal within 7 days, indicating excretion of excess water.

C. ELASMOBRANCHS. Salt concentration of elasmobranch blood is somewhat higher than that of marine teleosts but, similarly, lower than that of sea water. However, total blood osmoconcentration is somewhat higher than that of sea water because of a uniquely high concentration of urea and trimethylamine oxide (Städeler and Frerichs 1858, Suwa 1909, Smith 1931, Burger 1967, Forster 1967). The filtra-

tion rate of the glomerular kidney is high, but the osmotic inflow of water is not great and much of it is reabsorbed. The result is low urine output. As much as 95% of the filtered urea and trimethylamine oxide are also reabsorbed to contribute to the total concentration of the blood (Forster 1967). Salts diffuse inward because of their lower concentration in the blood. Some salts are excreted with the urine and some by way of the gills (Maetz and Lahlou 1966, Chan et al. 1967). However, the most important organ for excretion of excess salts is the rectal gland which secretes an almost pure sodium chloride solution (Burger and Hess 1960, Bulger 1963, Burger 1965).

Many elasmobranchs are euryhaline and their occurrences in fresh water are not uncommon, particularly in tropical areas where some live exclusively in fresh water (Smith 1936, Gunter 1942, 1956c, Herre 1955). The blood concentration of elasmobranchs in fresh water is lower than that of marine elasmobranchs largely because of a reduced urea content. Urist (1961) compared the serum composition of the freshwater shark *Carcharhinus leucas* of Lake Nicaragua with that of marine shark *C. leucas* and found that the total serum concentration of the freshwater shark is 83% and the urea content only 30% of that of the marine shark.

Even though the blood concentration of freshwater elasmobranchs is lower than that of marine forms it is higher than that of freshwater teleost fishes. The large concentration gradient between internal and external environments results in increased osmotic uptake of water and increased urine production over that of marine elasmobranchs. However, as pointed out by Hickman and Trump (1969), no new renal mechanisms are required. Since marine elasmobranchs are also somewhat hyperosmotic to their environment and have adequate glomerular surface, activity of mechanisms already present can simply be increased in dilute or fresh water. An increase in glomerular filtration rate with resultant increase in urine output results in increased rate of urea loss and reduced blood concentration. However, urea reabsorption is usually sufficient to retain a fairly high blood concentration in comparison to that of teleost fishes and to produce a urine that is hypo-osmotic to the blood. The completely landlocked ray, *Potamotrygon*, is unique among elasmobranchs in that it apparently does not reabsorb urea at all for the blood is free of this substance (Thorson et al. 1967).

In euryhaline elasmobranchs the filtration rate and tubular permeability of the kidneys can be varied to accommodate changes in environmental salinity, but the adjustments require time. Price and Creaser (1967) found that the skate, *Raja eglanteria*, requires 48 hours to reach osmotic equilibrium after only a 2.5 ‰ change in salinity, and 70 hours after a 10.0 ‰ change. Holmes and Donaldson (1969) postulate that elasmobranchs living in fluctuating estuarine conditions may never reach osmotic equilibrium.

Freshwater elasmobranchs living in waters with access to the sea, such as Lake Nicaragua and Rio San Juan, are thought to be recent immigrants. They retain a relatively high blood urea and are thought to be able to osmoregulate in sea water (Thorson 1967). However, certain groups show tendencies toward becoming stenohaline freshwater fishes. The lack of urea in *Potamotrygon* has been mentioned. The rectal glands are not needed for salt secretion in a freshwater environment, and

they have become degenerate and nonfunctional in Lake Nicaragua sharks (Oguri 1964).

OSMOREGULATION IN EURYHALINE FISHES

Most euryhaline fishes maintain a fairly constant blood concentration in all salinities (Potts and Parry 1964a). Some tolerance to internal change is required of certain anadromous and catadromous fishes as they migrate between the sea and fresh water. These species are able to osmoregulate to some extent in either medium and are never at isosmoticity for long. In general, the wide changes in environmental salinity tolerated by euryhaline species involve shifts between the osmoregulatory mechanisms used by marine fishes and those used by freshwater fishes. Many species require gradual adaptation to changed osmotic conditions, but some are able to adjust osmoregulatory processes very quickly. The tide pool blenny, *Blennius*, can change from sodium uptake to sodium excretion within minutes after transfer from fresh water to sea water (Hoese, vide Potts and Parry 1964a). Studies by Black (1948a) showed that the euryhaline killifish, *Fundulus heteroclitus*, adapts to transfer from fresh water to 100% sea water in only 6 hours. Copeland (1948) described histological changes in the chloride cells of *F. heteroclitus* that indicate a change in function from salt absorption to salt secretion within two days after transfer from fresh water to sea water. In view of Black's and Copeland's results it seems probable that some immediate but temporary response may occur in the interval between time of transfer and time of reversal of normal osmoregulatory processes. Such responses as reduction of glomerular filtration rate and temporary storage of salts in muscle have been described for other species (Black 1951a, Oide and Utida 1968, Hickman and Trump 1969). Rate of adaptation may be related to direction of transfer or to acclimation period. Although in Black's experiments *F. heteroclitus* adapted faster when transferred from fresh water to sea water, chum and coho salmon fry adapted faster when transferred from sea water to fresh water (Black 1951b). In both cases adaptation was faster when the transfer was made in the direction of the normal environment of the experimental animal. In the flounder, *Platichthys flesus*, the speed of adaptation to sea water depends on how long the fish has been in fresh water (Motais 1961).

Most euryhaline species have a glomerular kidney, but aglomerular species such as the toadfish *Opsanus* can withstand varying salinities. *Opsanus* occurs naturally in very low salinities, and *O. tau* can live experimentally in fresh water (Lahlou et al. 1969, vide Hickman and Trump 1969). The distal convoluted tubule may or may not be present in the kidneys of euryhaline fishes. Its presence presumably favors salt reabsorption in fresh water but it is absent in some euryhaline species (Edwards and Schnitter 1933, Trump 1968 vide Hickman and Trump 1969). Renal adaptation to salinity changes involves changes in glomerular filtration rate, in tubular permeability to water, and in salt reabsorption (also urea reabsorption in elasmobranchs). The kidneys of marine fishes appear to be more adaptable than those of freshwater fishes. Gunter (1956c) listed approximately ten times as many marine fishes collected in fresh water as freshwater fishes collected in sea water. It should be noted that, contrary to what might be expected, the fishes of hypersaline waters are euryhaline species rather than stenohaline marine species. Fishes adapted

to coping with fluctuating osmotic conditions appear to be better equipped to handle hypersaline conditions than species living in constant high salinities (Hedgpeth 1947, Gunter 1967a).

The general response of euryhaline fishes to increased salinities is reduction in glomerular filtration rate and resultant decrease in urine production. This response immediately reduces water loss and allows time for tubular changes to occur. The tubules become increasingly more permeable to water and increasing amounts are reabsorbed. In some species the glomerular filtration rate returns to near normal in time, but the urine flow remains low because of compensating water reabsorption (Oide and Utida 1968, Hickman and Trump 1969). The gills shift to salt secretion to compensate for diffusion of salts into the body from the more concentrated environment and the fish may drink the medium. Thus when a euryhaline teleost fish is in sea water it osmoregulates in the same fashion as a marine teleost.

When a euryhaline fish moves into fresh water it may reduce its drinking, but water is taken in by osmosis. Initially the urine becomes more concentrated because of the high rate of water reabsorption from the permeable tubules. However, the water permeability of the tubules becomes reduced, and salts can be reabsorbed with little water reabsorption. The result is excretion of increased amounts of dilute urine. The gills shift from salt secretion to salt uptake, and transformation to the same osmoregulatory processes used by freshwater fishes is complete.

Many euryhaline fishes show definite migration patterns. Some migrations are cyclic and predictable and are often related to spawning activity or to seasonal effects on salinity or temperature. Others are sporadic, although they are probably related to some environmental factor such as food supply.

A number of factors may influence migratory patterns. Migrations related to life cycles, such as movement of adults from one salinity to another to spawn, or return of the young from the spawning grounds, are stimulated by internal factors. There is little doubt that hormones are involved, but the effects of the various endocrine glands responsible for all the observed internal changes have not been identified.

Seasonal migrations are difficult to interpret because of coinciding physical changes such as temperature, day length, and river discharge. Seasonal variations in rainfall with resultant changes in river discharge cause fluctuations in the salinity of estuaries and movements of isohaline lines. Gunter, Christmas and Killibrew (1964) attribute the seasonal fluctuations of faunal assemblages in the northern Gulf of Mexico in part to the effect of alternating wet and dry seasons on salinity. Variations in river discharge may also be of importance to anadromous fishes which may make use of rheotaxis in locating mouths of rivers and in choosing one stream over another during the course of their migrations (Russell 1937, Vilter 1944).

In describing seasonal movements of fishes in and out of the bays of the Texas coast, Gunter (1945) pointed out that they coincide with temperature cycles. Although it is difficult to attribute such migrations to a single factor, temperature undoubtedly contributes to observed phenomena because of its effect on metabolism and therefore on active transport mechanisms. Temperature is known to affect

osmoregulatory ability. At low temperatures sodium and chloride levels in the blood increase in marine fishes (Pearcy 1961, Gordon et al. 1962) and decrease in freshwater fishes (Parvatheswararao 1967, Houston and Madden 1968), indicating inhibition of active transport mechanisms and decreased osmoregulatory ability. This effect has been verified in studies of euryhaline fishes. At low temperatures blood sodium and chloride decrease in freshwater adapted fishes (Toews and Hickman 1969) but increase in the blood of the same species adapted to salt water (Rao 1969).

Reduction in ability to maintain normal salt concentration of the blood would tend to stimulate movement of euryhaline fishes out of low-salinity waters at low temperatures, in accordance with observed mass movements out of Texas bays with the approach of winter, as described by Gunter (1945).

Fresh water with a high calcium content favors maximum invasion by marine species (Breder 1933). Calcium reduces permeability and, therefore, passive inflow of water and loss of salts. Active hyperregulation is not required, and even some otherwise stenohaline marine fishes enter such waters. A high calcium level probably accounts for the large number of marine species found in Florida fresh waters. Odum (1953), however, attributes their presence to the high chloride content of these waters.

Gunter (1945, 1947, 1957a, 1961a, 1961b) has reiterated many times the correlation of salinity with size of motile euryhaline animals, with the smaller sizes occurring in lower salinities. Many of the small fishes found in low-salinity waters are the young of species that live at sea as adults but exhibit the typical estuarine life cycle already described for large motile invertebrates such as crabs and shrimp. June and Chamberlin (1959) mentioned these questions with regard to menhaden. Spawning takes place in offshore waters and the larvae move shoreward to low salinities to feed and grow. After a time they return to the sea, and since their seaward migration is accompanied by growth, there is a direct relationship between size and salinity. The relationship is related to life cycle and might be considered behavioral. There is little doubt that a period of growth in nutrient rich waters where they may escape from less euryhaline predators is advantageous to young fishes, but the need to reach low salinities is more than behavioral. Physiological adaptations have developed that appear to require that early growth take place in low salinities. The ability of small fishes to tolerate greater dilutions than larger specimens may be related to size of gill area in relation to body size. Keys (1931) was able to correlate ratio of head length to body length with salinity tolerance in the Pacific killifish, *Fundulus parvipinnis*. He concluded that small fishes have a relatively larger gill area than larger ones and are better able to cope with the increased respiratory demands imposed by a dilute environment.

Hormonal influence on migration and osmoregulation is not clear. Observations of thyroid activity indicate that this gland is involved in adaption to varying salinities and in producing internal changes related to migration, but its control of osmotic processes is questionable (Koch and Heuts 1942, Hoar 1951, Kawamoto et al. 1958, Harris 1959). Because of the known role of the pituitary and adrenal glands in water and salt regulation in mammals, attempts have been made to demonstrate that these glands are involved in osmoregulation in fishes (Keys and Bateman

1932, Burden 1956, Pickford 1959). The results have been almost completely negative. However, Burden found that hypophysectomized *F. heteroclitus* dies in fresh water but not in sea water. He attributed the deaths to lack of some as yet unknown pituitary factor necessary to maintenance of the mucous cells of the gills. The fishes in fresh water lost considerable amounts of chloride, but the chloride secreting cells appeared unaffected, pointing to a protective role of the mucous cells.

Changes in osmoregulatory ability have been correlated with breeding activity in some studies. Gueylard (1924) and Koch and Heuts (1943) observed reduced tolerance to sea water during the breeding season in normally euryhaline sticklebacks which breed in fresh water.

Several workers have noted internal changes that might induce migration in anadromous and catadromous fishes. These species meet particularly complex osmoregulatory problems. Often they are stenohaline at a given stage in their life cycle, yet they must completely reverse osmoregulatory processes at some point as they pass from one osmotic extreme to another. The picture is complicated by species differences in life cycles and by different osmotic responses at different ages. Reviews of osmoregulation in anadromous and catadromous fishes are given by Black (1951a), Potts and Parry (1964a), and Hickman and Trump (1969). The variations in life cycles are too numerous to describe in detail here, but a few examples are given below:

(1) *Anadromous lampreys*. Except for the handling of divalent ions, lampreys in the sea and in brackish water osmoregulate in essentially the same manner as marine teleosts. As the adults ascend rivers to spawn they become less and less tolerant of sea water, and they finally become stenohaline freshwater fishes. They are more permeable than freshwater teleosts, but they handle greater water uptake by excretion of larger amounts of urine. Once they become adapted to fresh water they cannot return to the sea, and they die after spawning. Little is known of osmotic adaptations of the ammocoete larvae as they migrate seaward. Gordon (1968) states that they are euryhaline, but he gives no supporting evidence nor indication of the age at which they become euryhaline. Freshwater lampreys osmoregulate in the same fashion as freshwater teleosts.

(2) *Shad (Alosa sp.)*. Adult shad are unable to osmoregulate in fresh water. Their blood concentration falls as they migrate up rivers. Most individuals die after spawning, but some survive to make their way back to the sea. The latter survive changes in salinity because of an ability to tolerate changes in blood concentration rather than ability to osmoregulate (Fontaine 1930).

(3) *Salmonids (Salmon and trout)*. Salmonids vary in their life cycles and show corresponding variations in osmoregulatory responses. Most are anadromous, but some races complete their life cycles in fresh water. Examples are the rainbow trout, *Salmo gairdnerii* and the brown trout, *S. trutta*. They are typical freshwater hyperregulators but retain their ability to hyporegulate. When placed in sea water their osmotic behavior is no different than that of anadromous races of the same species.

Adults of some species of anadromous salmon die after spawning whereas others return to the sea. The Pacific genus *Oncorhynchus* does not survive after spawning but the Atlantic and Pacific *Salmo* does. The survival of the adults of some species and the death of others is not attributable to differences in osmoregulatory ability since blood concentration differs little in the two groups.

There are, however, differences in osmotic behavior of the young of various species which can be related to differences in life cycles. Comparative studies have shown differences in chum salmon (*O. keta*) and coho salmon (*O. kisutch*). Chum salmon migrate to sea immediately after hatching. The fry are euryhaline and can withstand transfer back and forth between fresh and sea water. Coho salmon, however, remain in fresh water for a year before moving seaward. The fry are stenohaline and can withstand direct transfer to salinities no higher than 14 ‰. When chum and coho fry are placed in sea water they both initially take on chloride ions. However, the chum fry soon begin to excrete these ions, and the blood returns to normal within 36 hours. On the other hand, coho fry continue to take on chloride until death occurs (Black 1951b). The development of a chloride secreting mechanism necessary to movement to the sea occurs at different ages in different species. Hoar (vide Black 1951b) found chloride secreting cells in chum salmon at the fry stage but was unable to discern them in coho salmon until they reached the yearling stage just prior to migration to the sea.

Keys (1933) and Copeland (1948) suggest that development of chloride secreting cells in euryhaline fishes is stimulated by increased blood chloride due to increased environmental salinities and subsequent drinking of sea water. However, the development of these cells is not environmentally induced in young salmon since they develop prior to migration while the fish is still in fresh water. Rather, their development is controlled by some internal factor or factors which produce changes that, in effect, seem to force the young fish to seek higher salinities. In addition to increased salt loss due to development of chloride secreting cells, salmon have been found to lose body fat or show a change in type of fat at the time of smolt metamorphosis. There is an increase in cholesterol/fatty acid ratio which is postulated to result in tissue imbibition of water (Lovern 1934). Increased water uptake coupled with increased salt loss could stimulate young salmon to seek a more concentrated environment. Similar changes have been noted in the adult eel just prior to its seaward migration (Fontaine 1948). In summary, adult salmon enter fresh water to spawn but they vary in their ability to return to the sea. Young salmon vary in the time spent in fresh water and in the development of chloride secreting cells.

(4) *Eels*. Eels are euryhaline from the elver stage, the time at which they reach coastal waters, until maturity (Firly 1932). The freshwater adults have low permeability to water, and the glomerular kidneys are able to handle water excretion with low urine output. The kidneys must also function in almost complete reabsorption of salts since the gills, though effective in salt secretion, are ineffective in chloride uptake (Krogh 1937). As in young salmon, adults ready to migrate from fresh water to the sea exhibit chloride loss and reduction in fat (Fontaine and Callamand 1940). Nothing is known of the physiology of adults after they migrate to sea to spawn or of the early leptocephalus larval stage.

Freshwater fishes that are sometimes found in estuaries are not truly euryhaline. Their appearance in the estuary is usually correlated with periods of heavy rainfall or some other condition that reduces the salinity. Most freshwater species can tolerate environmental salinities no higher than their normal blood concentration, and few preferentially choose to leave fresh water at all. Certain species, however, are regularly found in inshore estuarine waters. A notable example is the alligator gar, *Atractosteus spatula*, of the Gulf coast. The heavy ganoid scales together with the somewhat reduced gill area in relation to body size of this air-gulping fish probably make it less permeable than most freshwater teleosts.

Stenohaline marine fishes cannot ordinarily withstand salinities lower than their normal blood concentration. Migrations into estuaries are correlated with seasonal variations in salinity or periods of unusually high salinity due to droughts or other factors. The movement of marine fishes into fresh waters of high calcium content has already been mentioned. These fishes are not strictly euryhaline in the general sense of the word.

In summary, as stated by Gordon (1962), the euryhaline lampreys and teleost fishes are excellent osmoregulators and can generally hold within 10% of constancy over a range of 0.1 to 31 ‰. About 90% of the osmotic regulation concerns NaCl. The blood salt concentration of the elasmobranch fishes (Chondryichthyes, sharks and rays) are comparable with those of other fishes. Additionally, they have a high blood content of urea and trimethylamine oxide which raises the osmotic pressure to hypertonic even in sea water. By dropping this organic concentration in ways unknown, many species become euryhaline. They can drop excessive salt loads by excretion through rectal glands.

OSMOREGULATION IN VERTEBRATES OTHER THAN FISHES

Included among the relatively few tetrapods that have invaded marine or brackish waters are various species of turtles, crocodiles, iguanas and water monitors, certain snakes, whales and other cetaceans, seals and their relatives, and some amphibians. A number of birds are also classed as marine.

Except for the amphibians, these animals are all hypo-osmotic air breathers with internal respiratory surfaces. Few amphibians are truly marine, but several species of toads and frogs enter brackish waters. Their permeable skins pose osmoregulatory problems not faced by other tetrapods, and the problems are not solved in the same way by all amphibians. The European green toad, *Bufo viridis*, withstands salinities up to 19 ‰ by tolerating increased blood concentration with increased salinity (Gordon 1962). The major substances contributing to the increased blood concentration are sodium and chloride. A different adaptive mechanism is used by the frog, *Rana cancrivora*, which inhabits mangrove swamps of southeastern Asia. *R. cancrivora* can withstand even higher environmental salinities than *B. viridis* (up to 28 ‰). The salt concentration of the blood is lower than that of the surrounding water, but the total osmoreconcentration is increased by a high urea content (Gordon et al. 1961). Thus, this frog osmoregulates in much the same manner as elasmobranch fishes. Since the urine salt content is low in spite of inward diffusion of salts, an extrarenal pathway for salt excretion must exist.

In this country the salt water Reptilia are the diamondback terrapin, from Cape Cod to south Texas, the alligator from Virginia to Texas and the American crocodile in south Florida. Generally these animals move in and out with the salinities they prefer and which nobody knows much about. The crocodile is more of a salt-water animal than the alligator, but the alligator has been seen swimming a mile out in the Atlantic off South Carolina and large ones are sometimes taken in trawls off the Louisiana coast. Water moccasons are commonly found in brackish water marshes, such as around the Gulf Coast Research Laboratory, but no one knows exactly what the salinity influences are. Most probably they are all indirect.

There are also four species of marine turtles that haul out on the sea beaches to lay eggs from South Carolina southward. Occasionally, some of these animals are found in the lower bays. Presumably, they are never hurt by salinity changes unless heavy rains wash down the beaches and destroy the eggs by wetting them, washing them out or packing the sand so the young cannot get out after they hatch.

After heavy rains and flooding the senior author once picked up a common snapping turtle swimming at the mouth of Biloxi Bay. The salinity record was lost. Following a harsh drought on the south Texas coast, from 1948-1958, the diamond-back terrapins of the brackish waters of Copano Bay were forced to leave because their environment became hypersaline, up to 61.0 per mille. They made their way some forty miles to the coastal passes where, being in a weakened condition, some were captured by hand and kept for a few years on the dock laboratory of the Institute of Marine Science at Port Aransas.

Marine reptiles and birds have orbital or nasal salt glands that are histologically and functionally similar to the rectal glands of elasmobranchs. They, too, secrete a concentrated sodium chloride solution, thus allowing excretion of salts with minimum water loss. Birds further conserve water by excreting a hyperosmotic urine. The kidneys of marine reptiles and birds are unable to excrete large salt loads and thus these animals would die in high salinity environments were it not for the extrarenal pathways for salt excretion.

The blood of birds and reptiles, as well as that of mammals, is hypo-osmotic to sea water but since all these animals are impermeable, they do not face a need to get rid of excess salts taken in by diffusion. Although water loss is kept at a minimum, some is lost in excretion of nitrogenous wastes and from the lungs and must be replaced. Presumably, the salt glands of marine birds and reptiles could handle excess salts taken in by drinking sea water but with the exception of the albatross, these animals are not known to drink sea water. Their methods of handling excess salts and of replacing lost water are not clear. Mammals that feed on fishes have the advantage of osmotic work already done by their prey; that is, their food has a salt content nearly the same as that of their own body fluids. Those that eat invertebrates, however, take in food of nearly the same concentration as sea water. Some scientists have not ruled out the possibility of an extrarenal structure for secreting salts (Fetcher and Fetcher 1942, Potts and Parry 1964a). Others believe that the hyper-osmotic urine produced by mammals is sufficient to handle excess salts. Some workers have made calculations which indicate that marine mammals can maintain osmotic equilibrium on either a fish or an invertebrate diet with no other water source and without extrarenal salt secretion. Calculations have been

made for seals (Irving et al. 1935) and for whales (Krogh 1939).

There are four marine mammals that invade the bays on the Gulf. One is a small unidentified porpoise known as the dog porpoise, which is seen occasionally and which some of us have been after for years, but none has been captured, at least by a cetologist. California sea lions have been reported from eastern Canada to Miami and several locations in the Gulf (see Gunter 1968). They could undoubtedly establish themselves on the Atlantic coast, but the escapees are generally persecuted until they die out. The bottle-nose dolphin, *Tursiops truncatus*, is the common marine mammal of the United States coast. They invade rivers for a few miles, but they do not stay. In the Gulf they are seldom seen beyond five miles offshore. However, in the Atlantic off Florida some stay so much offshore that they develop large parasitic copepods and barnacles like the whales, while others in bay waters never have these parasites (Caldwell and Caldwell 1972).

It is well known that the manatees, *Trichecus manatus*, which live on the marine grasses of Biscayne Bay spend their resting time in the Miami River in downtown Miami. Biscayne Bay has approximately the salinity of full sea water. No doubt this salinity change prevents fouling growths on manatees.

As far south as North Carolina the harbor porpoise, *Phocaena phocaena*, comes into the bays and still farther north, in New England, the Harbor seal, *Phoca phoca*, comes in. But the salinity relationships are unknown.

SOME RELATIONS OF AQUATIC PLANTS TO SALINITY

The great efflorescence and diversity of plant species is on land and not in the sea, in spite of the fact that more photosynthesis probably takes place in the sea. In the sea there are the diatoms, dinoflagellates, red and brown algae, a few green algae and that is about all. The flowering plants are minuscule in number and those that will grow with their roots in the water are not numerous relatively, but they form the vast marshes at the edge of the ocean.

The osmotic relationships are largely unknown. There are no organ systems for salt excretion and ordinarily the cells cannot swell in hypo-osmotic solutions because of the thick cell walls, but there are salt glands present in certain vascular plants. Some vascular plants withstand high salt concentrations in the soil water solution by passing the salt water through the plant and out through salt glands located on the leaves. Others compensate by increasing the salt concentration in the internal solution of the individual cells and thus become succulent. The mechanism by which the remainder are able to tolerate hypersaline solution is unknown. We know something about the salinity ranges at which the few salinophile plants will live, but even this type of information is scarce.

The Louisiana Marsh, of which the east Texas and Mississippi marshes were until recent years unbroken and continuous extensions, is the largest in the world. Characteristics of it were described by Penfound and Hathaway (1938) and O'Neal (1949). Unfortunately this marsh is declining rapidly and wasting away at about 17 square miles a year in Louisiana because leveeing of the Mississippi River has cut off its sediment supply. A quantification of the loss for one area was given by

Eleuterius (1971). The importance of marsh areas is now becoming recognized everywhere and the state legislatures of coastal states are struggling with protective measures. Odum (1961) maintained that 60% of Georgia's estuarine productivity came from the low marshes.

In recent years certain aspects of the Mississippi marshes have been examined by Eleuterius (1972b). He has found that there are 66,931 acres of marsh; the mainland contains 63,982 acres of salt marsh and 823 acres of freshwater marsh; of the salt marsh 96% is dominated by *Juncus roemerianus*, *Spartina alterniflora* 3%, *S. patens* 0.7% and *Scirpus olneyi* 0.1%. The barrier island marshes were found to be of lower salinity than the surrounding water. He found further that *J. roemerianus* increased in density but the leaves were shorter in length with increased salinity. Hypersaline soil water conditions however, produced dwarf plants. The increase in density was attributed to the removal of competitive species from these regions of the marsh.

Another salinity factor was a determination of 400 grams per square meter of freshwater marsh plants and 2 kilograms for a saltwater marsh, as standing crop, which was also very close to the annual production. On a dry weight basis the maximum annual production of Mississippi marshes was estimated at more than three million tons.

Eleuterius (1972b) reported that there were over 300 species of vascular plants in the Mississippi marshes and said, page 155, "Each estuarine system sampled showed a progressive increase in vascular plants from saline to freshwater." This is a reverse gradient from that reported in animals, but it is a reflection of the fact that the higher plants in general are salinophobes, especially with regard to sodium chloride. He found that during the spring and early summer the plants generally found in fresh and low-salinity waters, extended far into brackish and upper saline marsh due to the abundance of fresh water in the spring. "The fluctuation in plant distribution over the salinity gradient was a response primarily to changes in salinity."

Eleuterius (1972a) has also studied the flowering submerged plants in Mississippi Sound using the transect method. About 20,000 acres are covered with plants. Grass beds are mostly inside the barrier islands. *Vallisneria americana* occurred in the shallows of rivers and upper bayous; *Ruppia maritima* was found along muddy shores of shallow bays and bayous. North of the barrier islands, turtle grass, *Thalassia testudinum*, was next offshore and manatee grass, *Cymodocea manatorum*, was found at depths of 4 to 6 feet. Some beds were mixed with all three species.

Around Cat Island there was an area of shoal grass and algae and algae alone some 4 to 6 square miles in extent. This consisted of mostly red, fewer brown and very few green algae.

After this was written a summary paper by Earle (1972) on benthic algae and seagrasses of the Gulf of Mexico just came to hand.

SOME EXAMPLES OF COASTAL WORKS CAUSING SALINITY CHANGES AND THEIR EFFECTS

Various activities occur from time to time along or near the coasts which result in temporary or permanent changes in the salinity of coastal waters over considerable areas. These changes may be unheralded or unrecognized and in the long run they are forgotten. The history of the structural works are usually buried in the stored files of a Corps of Engineers District Office, and are sometimes difficult to unearth. Nevertheless, certain instructive examples are worth examination and we have perforce selected some which became known to the senior author over the years. The documentation is not complete, but the cases are essentially correct as described.

The Laguna Madre of Texas and its connecting bays, Baffin and Alazan, were notorious for high salinities and heavy fish-kills for many years prior to the 1940's. Salinities up to 112 ppt were reported and every ten years or so before the 1940's a vast destruction of fishes took place. Porpoises did not venture into the area, blind fish from the Laguna were often reported in South Texas and the higher Crustacea, shrimp and crabs, were extremely rare or absent in the immediate area. On the other hand, it produced large amounts of a few species of fishes and molluscs.

The senior author discussed certain hydrographic features in an article for laymen and Hedgpeth (1947) gave the first professional description of the area. Both of us opposed the virtual damming of the upper Laguna by a dirt causeway with only the proposed Intracoastal Waterway as the exchange area between the Laguna and Corpus Christi Bay. We thought the high-salinity problems of the Laguna would become devastating. Instead, as soon as the Waterway was dug the length of the Laguna down to Brazos Santiago Pass, the whole situation grew better and there has not been a big fish-kill in the Laguna Madre since then, even though a 500-year drought occurred from 1948 to 1958. The salinities in the Laguna have been materially reduced. The reason for this beneficial effect of the Waterway is the high head of water maintained in Corpus Christi Bay by the steady southeast winds. This causes an almost continuous flow southward through the Waterway, flushing the Laguna out through Santiago Pass.

The Laguna Madre is still a high-salinity area but not a lethal one. Its biological characteristics have been described in some detail by Simmons (1957).

In 1932 a sentient operator contracted to clean out the log raft in the lower Colorado River of Texas, which at that time entered Matagorda Bay at the town of Matagorda. This impediment to free flow of the river caused flooding for the lower 20 to 30 miles of the stream, including the county seat and courthouse, which had been built within the natural floodway of the river, as human structures often are.

Dynamite was placed at strategic places and exploded just in front of a flood bearing down upon the lower river. This action was highly successful. Enough of the raft was loosened and shoved out to allow the force of the water to loosen the remainder, after which the river also removed large amounts of sediment. In short, the lower delta was removed from the mainland and spewed out into the narrow

east arm of Matagorda Bay. Within three weeks time it crossed the bay and breached the offshore island, commonly and erroneously known as Matagorda Peninsula. In the process Mad Island, Dog Island and Tiger Island oyster reefs were covered with mud. These reefs produced approximately one-fourth of annual oyster production of the State of Texas at that time. They were later dug up as mudshell or dead reef shell by Parker Brothers Dredging Company. The process went on so fast that soon after a blacktop road was laid down the east bank of the river, passing in one place an almost buried navigation marker which said "This channel is 14 feet deep."

Needless to say the fresh water and nutrients which formerly emptied into Matagorda Bay and enhanced its productive estuarine nature now enter largely into the open Gulf where they are dissipated quickly by the highly saline waters. Actually the whole event amounted to a speeding up of a geological process. The Brazos River to the east of the Colorado had gone through the same process naturally and emptied into the sea at the time the Europeans came to Texas. Nevertheless, mankind probably always loses when the rivers are prevented from building up their floodplains.

Later on, locks had to be constructed where the Intracoastal Waterway crossed the Colorado River because the water levels were not often the same. Quite often this permitted large amounts of fresh water to flow westward. During the 1940's the Waterway was cut along the edge of Oyster Lake, which was a blind body of water with one opening into the main part of Matagorda Bay, and highly productive of oysters. It turned fresh quickly and the Oyster Lake Reef died and silted over. The same thing happened to Deep Reef just off Oyster Lake in Matagorda Bay. Two good oyster reefs were destroyed through lack of understanding of the effects of freshwater flow.

Three great environmental changes have taken place since this continent was settled by the European. The first was the destruction of the solid hardwood forest east of the Mississippi by the subsistence farmer—not the lumberman—the farmer. The second was the agriculturization of both the short and tall grass western prairies and the destruction of its animals, the chiefs of which were the buffalo and its Indian predator. The third, and possibly as important as the others, has been the leveeing of the Mississippi River and its occlusion from its floodplain and valley. The following quotes are from Gunter (1952):

"The alluvial plain includes both the floodplain and the alluvial plains which are not covered by flood waters. Streams of the valley have large stage variations and in their natural state periodically overflow their banks. Sediments deposited on the banks by high water form natural levees sloping away from the river at a gradient of about seven feet to the first mile; thus large flood basins, which are cut off from the channel at low water stages, exist between the river and escarpments of the valley. The river and its tributary streams drop sediments in these basins and aggrade the valley. The Mississippi floodplain covers 35,000 square miles, including 15,000 square miles of deltaic plain.

"The Mississippi watershed is exceeded only by those of the Amazon and the Congo and covers 1,224,000 square miles of approximately one-third of the United States and 13,000 square miles of Canada. The average annual rainfall over this area

is about 30 inches, of which about one-fourth travels to the sea by way of the river. The annual water discharge at the mouth of the Mississippi has been estimated at 785,190,000,000 cubic yards and the sediment carried into the sea is between 1,000,000 and 2,000,000 tons a day."

"Russell and Howe (1935) have pointed out that the Mississippi River may be termed the 'Father' of Gulf coast geology and geomorphology. It has a commensurate relation to the estuarine life of the region" (Gunter 1952). Le Page du Pratz (1758) the engineer for the early French colonialists stated it differently, saying Louisiana is a land that "is gathered from the sea."

According to Gunter (1956a), "The annual flood made levees necessary from the time of the first settlement of the white men in Louisiana. The first levee of the Mississippi River was constructed around the City of New Orleans when it was founded in 1717. It was not completed until 1727. This was in the area known as the *Vieux Carré* or now the French Quarter. The levee was 5,400 feet long and built in the form of a quadrangle because there were no adjoining levees up and down the river and the protected area had to be completely enclosed to prevent the backwaters from coming in behind. The levees were only about three feet high, which was sufficient in that day. It was called in French 'banquette.' The enclosed area was often muddy and impassable to pedestrians, who walked instead upon the higher ground of this low levee. For that reason the people of New Orleans to this day refer to their concrete sidewalks as 'banquettes.' This beginning of the levee system and the long fight against the river, which has now been carried on for two hundred and forty years, was so small and weak that, as an indicator of future events, it can scarcely be said to have cast its shadow before."

"More and more the banks of the main river, and finally its tributaries, were leveed. Maps of the present system, show a complicated tracery and the total levee system now exceeds 2,500 miles. The floods grew ever higher as the river was cut off from its flood basins and, in the lower river, from its distributaries (see Gunter 1956a). The Carrollton (New Orleans) gauge registered 14.95 feet in 1882, 16 feet in 1890 and 21 feet in 1912. The greatest flood of all came in 1927, when numerous crevasses in the lower river modified flood heights, making them useless for comparison."

"The flood heights have increased simply because the river has been cut off from its vast overflow areas, which formerly covered 35,000 square miles. The river, probably due to its faster flow and straighter channels, has, if anything, incised its bed and is probably deeper than ever before."

"In the southern reaches at least, the river was formerly filled with aquatic life, not only within itself but along the channels, bayous, lakes and swamps nearby. It was the habit of most of this aquatic life to spawn in the spring, and live in the quiet backwaters, rather than the swift and muddy main stream. No one actually knows what is now in the river for a biological study of it has never been made, but the effect of flood control on the life in the main river has doubtless been quite harmful. Within the swamps and former overflow areas the effect has also been bad and this question is much more important than the life of the main river itself. The swamps have not been wholly destroyed. Some of them remain, although they are

going. There is quite enough land left in the United States so that people do not have to live in drained swamps, with all of its attendant problems. Therefore, I do not count living space or living room as good causes for the draining of the swamp.

"Years ago Viosca (1927) pointed out some of the advantages which would have accrued if the white man had, in the beginning, started out to live with the river instead of fighting it. His concern was with aquatic resources, both fresh water and marine, in the State of Louisiana. The problem is larger than that, but the ideas presented here are an extension of his. Living with the river entirely from the beginning would have involved building all houses on low stilts, with low levees only around cities on the flood plain. Thus the river would have spread out naturally every year without harming the human population or the property along its banks.

"The Mississippi River is one of the greatest resources on this continent. Yet it is sometimes paraphrased, and looked upon, as America's sewer. It is used as a sewer, as a local water supply and a navigation channel. Its more bountiful resources are not used. It should be used as a land builder, a supplier of water for vaster areas and as a creator of wildlife and aquatic resources. The river should be given back some of its overflow basins, all that can possibly be spared, and not canalized so that it hurries ever faster to the sea with its great load of the continent's soil.

"In spite of lack of knowledge of specific problems, it seems clear that a broad program of River Use, in all of its vastly beneficial potentialities, should supplant flood control alone and opposition to the river. Such a program would slowly enhance and upbuild all life along the banks of the Father of Waters, including human society. To use the language of another day, it would increase human felicity on earth, at least in the Mississippi Valley."

With regard to coastal salinities, the levees are still being built right to the mouth of the river due to Louisiana laws which cast doubt upon the ownership of areas not behind a leveed section of the river. The present situation funnels water out of the river and starves the adjacent areas, so that the oyster areas close by are dying. By the same token the marshes are eroding away. Over in the Atchafalaya area only is land building up, and there an estuarine area with extensive oyster reefs is being created in the open sea. It has not been documented yet in print, but the dichotomy of water flow exists and the continuous fanlike delta feeding the whole Louisiana and Mississippi coast no longer exists. The estuarine area which supports the largest fishery in North America is diminishing not through decline of water flow, but its misdirection.

About one-fourth of the river floodplain remains. It would seem that an economic and ecologically dirtwise program of saving this part of the Earth by reverting the floodplain to its river is of the highest order.

A small part of the Mississippi River problem is that of the Bonnet Carré Spillway—named for a small red cap the French liberals used to wear, called a "Square Bonnet." It is scheduled to overflow or to be opened when the Carrollton flood gauge reaches 20 feet. This is set to reduce the flood pressure against the New Orleans levees, where under the docks, wharves, storage areas, etc., the official trust is not complete.

This spillway has been opened three times, in 1937, 1945 and 1950. The senior writer (Gunter 1953) studied the 1950 opening carefully. The 1937 and 1950 openings were beneficial. They began in February and ended in March and never got above 220,000 second-feet or a total of 12,000,000 acre-feet. The 1945 opening began in March and ended in May. It attained a flow of 320,000 cfs and almost 30,000,000 acre-feet. The exposure to low salinity was longer, more intense and at a higher temperature than at the other openings. The effect was described as devastating. In other words, it caused a catastrophic mortality, of oysters and associated organisms, which the other two openings did not cause (Gunter 1953, Viosca 1938).

The oyster production in New Jersey, which came from Delaware Bay, ranged from about 7 to 10 million barrels from 1880 to 1931. In 1932 this production was reduced about one-half, and it remained so until 1956 when it fell sharply again. The present production runs about 70,000 barrels or less.

New Jersey was one of the main oyster production states of the United States and during some years it ranked very close to the top. This stepwise decline was caused apparently by the diversion of the river water, which normally flowed into Delaware Bay largely to the City of New York. This was done by Federal court order. Now the oyster industry in the State of New Jersey is virtually a thing of the past. These developments were opposed completely by the late Dr. Thurlow C. Nelson, the dean of American oyster biologists at that time, but his efforts were to no avail for the needs of the oysters could not prevail over those of the people of New York City. The oyster statistics, which are the remaining evidence and data in this development, are given in Lyles (1965).

SOME GEOGRAPHIC CONSIDERATIONS

The northern and western Gulf of Mexico along with the area from about Cape Canaveral, Florida, to Cape Hatteras, North Carolina, is quite similar in its fauna. This area is known to the zoographers as the Carolinian. This area is also labeled by the climatologists as subtropical, wet, cool. In its inshore areas this region is biologically characterized by oysters, menhaden and blue crabs in the estuaries in addition to the shrimp and croakers.

It is best characterized in its offshore or shallow waters as being dominated by the penaeid shrimp and by the croaker family of fishes, the Sciaenidae. In this region most of the estuarine organisms have the characteristic life history described before, in which the adults spawn offshore in high-salinity waters and the young make their way into the estuaries to grow up. When the estuaries change salinity due to droughts or to floods the fauna changes and some of it will die out, only to be reconstituted when conditions change to normal. This area changes to a tropical marine fauna at about the southern end of the Indian River on the east coast of Florida, and at about the Caloosahatchee Estuary on the west.

This is the area of the big estuaries for the United States coast and it is the area of greatest fisheries production. The most productive of all is the stretch around the Mississippi River, which has been previously called the Fertile Fisheries Crescent (Gunter 1963).

Papers from the University of Miami concerning Whitewater Bay and the southern tip of mainland Florida, plus others concerning Biscayne Bay, have characterized the tropical area at the end of the Florida Peninsula. Salinity change will not be great in southern Florida except for hurricanes and manipulation of the waters of Lake Okeechobee. The papers of Springer and Woodburn (1960) and Gunter and Hall (1965) describe the west coast in the transition zone between the tropics and subtropics. The east coast transition zone is described by Gunter and Hall (1963).

The northern and west coast of the Gulf are described by papers emanating from the Institute of Marine Science at Port Aransas, Texas. Menhaden, shrimp and to a smaller extent crabs and oyster fisheries are typical of the Carolinian region.

Northward from Cape Hatteras things change rather abruptly faunistically to temperate zone. The shrimp disappear although the menhaden, blue crabs, and the oysters remain. The general fisheries population changes and there are even records of lobsters taken offshore from Chesapeake Bay. The various clams and the striped bass become more important in the fisheries. The inshore waters from the Carolinas to the middle Atlantic states are particularly noted for the shad fisheries, the elements of which run up the rivers in typical anadromous fashion. The middle Atlantic states have been characterized marine biologically by Hilderbrand and Schroeder (1928) and the various shorter papers that have come out from the New Jersey contingent of oyster workers and more recently from the Chesapeake Bay laboratories of Virginia and Maryland. In recent years the Virginia Institute of Marine Science has turned out many papers. Over the years a number of papers from the two university laboratories and one Federal laboratory at Beaufort, North Carolina, have described this area.

This temperate area of coast extends roughly from Cape Hatteras to Cape Cod. To the north of Cape Cod the water becomes cooler. The offshore fauna has been characterized by the papers of Bigelow (1924) on the plankton and Bigelow and Welsh (1925) on the fishes of the Gulf of Maine. In general the cod and their relatives are more abundant offshore.

One good guide to the fauna of any local area is the Fisheries Statistics of the United States which has been published annually by the National Marine Fisheries Service and its predecessors with more appropriate cognomens, the Bureau of Commercial Fisheries and the Bureau of Fisheries.

The northern region, the cool temperate zone, is characterized by its lobster and herring fisheries and particularly by the cod and cod-related fisheries of the offshore waters, recently becoming greatly overexploited because of foreign fishing boats. Unfortunately, especially in the lower New England region, pollution is such over-riding consideration that salinity changes do not amount to much.

The Pacific coast of the United States, south of Alaska, is cool temperate and south of San Francisco Bay it is dry. Thus there are no estuaries south of there on the California coast and as Hedgpeth pointed out, they are scarce on the Pacific coast. Nationally there are only two worthy of the name. These are Puget Sound and San Francisco Bay and there is or was a fairly characteristic estuarine fauna among which was a caridean shrimp *Crango nigricanda* that supported a fishery

forty years ago. However, land filling and pollution have changed this whole area considerably and today the only shrimp produced is *Artemia*, which is really not a shrimp. It supports a thriving industry around the salt pans because it is used by the ever-expanding pet fish and aquarium industry as food for young aquatic organisms. This region has been extensively studied by the California Department of Fish and Game under the title of Ecological Studies of the Sacramento-San Joaquin Estuary (Skinner 1972). This constitutes the largest most extensive estuarine study on the West Coast. The area is of particular importance, and changing because a so-called "Peripheral Canal" will carry much of northern California water southward to drier regions of the state. Up and down the Oregon and Washington coast there are small estuaries such as Willapa Harbor and Grays Harbor, where oysters grow, as they also do in Tomales Bay, California.

The so-called Columbia River estuary is a misnomer. This area is merely the lower part of the river, where salt water comes in and extends upstream as far as thirty miles on the bottom or goes away completely during high water. The situation works back and forth.

In fact there is none of the great faunal exchange movement in and out of the bays, estuaries and the production of vast fisheries in the nursery waters such as we have on the South Atlantic and the Gulf coast of the United States. Similarly there is not a great deal of information upon the salinity limits of the Pacific coast animals and a search for this information is quite frustrating.

The situation is such that Hedgpeth (1968) remarked that the chief environmental factor in the estuaries is the absence of the pounding surf, and that may well be true. The very fine book "Between Pacific Tides" lists the habitat and a great deal about biology of almost all of the organisms that will be encountered on the Pacific coast, but it gives only such information as "found in low salinity waters," etc. This book, an original product of Edward Ricketts and Jack Calvin, is becoming more and more a contribution of Hedgpeth, wherein he has fleshed out considerably the original conception. It is a pity that similar works for the Gulf and Atlantic coasts do not exist. We might say, however, that the book by Gosner (1971) covers part of the ground but not in the similar fashion. On the other hand he gives a good bit more information on salinity, probably because on the East Coast it is more important in the large estuarine areas.

The recent book by Remane and Schlieper (1971), "Biology of Brackish water," is the most complete of all on the ecology and physiology of the organisms in low-salinity waters and no student of these areas and organisms can neglect this important source book by two men who did so much to establish knowledge in the field. For generalities it is excellent, but data concerning specific organisms are different from the United States coasts because there is small overlap in species. The vast size of the Baltic estuarine area as compared to our coastal bays also presents a somewhat different situation.

SOME GENERAL REMARKS

There are some coastal areas of the United States where there is little land

drainage and, therefore, relatively high salinity, but such waters comprise only a small part of the coastline. They support a variety of species but the species do not occur in great abundance nor do they include the many commercially important species found in estuaries. The effect of man on life of the sea is much more likely to be exerted on estuarine forms, since areas of heavy population tend to be around streams and areas where streams enter the sea.

Upsetting of the ecological balance of an estuary, or estuarine pollution, can take many forms including sewage, detergents, insecticides, factory effluents of various kinds, thermal pollution, siltation, changes in salinity, and changes in circulation patterns. Salinity effects are more likely to be overlooked than some of the more obvious and more publicized effects. Yet dilution of salt water by excess fresh water and vice versa can have a definite and sometimes drastic effect on the flora and fauna of the area affected. Seldom are there massive fish-kills from changes in salinity. Only a sudden or drastic change that does not allow time for migration or for adaptive osmoregulatory processes to take place will actually produce mortality in adult euryhaline fishes. However, there can be greater effects on the young fishes with less mobility and less well-developed powers of osmoregulation. If the young fishes which use the estuarine areas as nursery grounds are not killed directly, changes in salinity that affect their food supply such as worms, shrimp, small crabs, and so forth, will just as effectively banish them from their former habitat.

Coastal projects of various kinds may modify the salinity of estuaries. They may change the proportions of salt and fresh water, affect the timing of salinity changes, alter water circulation patterns and flushing, or even convert former marshlands into freshwater ponds or lakes. Impoundment of marshes for mosquito control or construction of coastal highways that cut off marshlands from the sea can turn these important nursery grounds for marine fishes into freshwater bodies of water. Rerouting or enlarging of channels can change water flow patterns, and rerouting of rivers or withdrawal of water from them for irrigation purposes reduces the freshwater inflow into estuaries. Water control or flood control projects affect not only the amounts of fresh water entering an estuary but also the timing. Sudden dumping of large amounts of fresh water into an estuary on an irregular basis does not have the same effect on living organisms as gradual, cyclic seasonal changes which allow time for migration or gradual acclimatization.

Estuarine species are, by the very nature of the normal physical characteristics of an estuary, tolerant of short-term, moderate changes in salinity. But either large scale changes for a short period of time or lesser changes for a long period can change the kinds and distribution of organisms. If the changes are drastic and frequent, the areas involved may become uninhabitable by either saltwater or freshwater species.

There is still a great deal of information to be gained about the salinity relationships of most marine organisms. The salinity ranges for most of them are unknown and the salinity preferences, and how this varies with life stages, are known precisely for only a few species. Even so, considering the large number of species of organisms, what we know about them altogether seems to be almost overwhelming. For that reason we have tried to hold to principles. Individual species have to be considered and we have used the phyletic approach. This is reasonable

because the various phyla differ quite considerably in their salinity relationships. But finally, this report will not solve the problems of the engineer. We hope that it will open the literature and present some ideas to the biologists who must be called to make predictions or give judgments concerning the effects of salinity changes.

Coastal projects are not necessarily harmful. When properly planned and managed they may be beneficial. Gunter and Hall's study (1963) of the effect of St. Lucie Canal on St. Lucie Estuary of Florida showed no harmful effects on commercial fisheries or low-salinity sports fishes. The high-salinity sports fishes that move into the lower estuary when the floodgates are closed are temporarily driven out when the gates are opened. But this effect is more than compensated for by the bringing into the estuary of nutrients that can be used by small food and bait fishes and the young of sports and commercial fishes which are normal inhabitants of estuaries. The importance of estuarine areas as nursery grounds for a number of marine species, particularly the Atlantic and Gulf coasts of the United States cannot be overemphasized. Such areas are essential for completion of the life cycles of a number of commercially important species. Cronin et al. (1969) pointed out that flood control measures which increase the salinity of bays may destroy certain commercial species such as oysters but, on the other hand, increasing the salinity of low-salinity bays may increase their productivity of useful saltwater species. Viosca (1938) and Gunter (1952, 1953) commented on increased production of commercial species following opening of the Bonnet Carré spillway of the Mississippi River.

Coastal engineering projects have the effect of modifying the composition and distribution of living organisms. Although general guidelines for evaluating their effect may be set up, every estuary is a complex ecological entity and, as pointed out by Cronin et al. (1971), each must be studied as carefully as possible, and predictions of possible effects must be based on specific knowledge of the particular area involved. Such studies require coordination between engineers and biologists as well as preconstruction and postconstruction ecological studies. In this manner, increasingly more useful guidelines for the Corps of Engineers may be established, and understanding of estuarine systems may be increased. Engineers and biologists will have to work together to solve specific and finite problems in any local area for all of these are different in physical and biological characteristics.

ACKNOWLEDGMENTS

We are much indebted to Dr. Sewell H. Hopkins, of Texas A&M University, who has worked up an "Annotated bibliography on effects of salinity and salinity changes in coastal waters," based mostly upon material in the Texas A&M University Library. It contains 1,416 items and by no means pretends to complete coverage. However, it is a fairly broad and selective summary on animal salinity problems of the coastal United States. This was placed on large cards in alphabetical order by author and it has been cross-indexed by general subject matter and by phyla and classes of the Animal Kingdom. We have used the Hopkins bibliography particularly on all animal groups other than Mollusca, Arthropoda and Chordata on which we have utilized mostly our own material.

Dr. Adrian Lawler, of this Laboratory, pointed out some references we had not seen.

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